RELATIONSHIPS OF HABITAT PATCH SIZE TO PREDATOR COMMUNITY AND SURVIVAL OF DUCK NESTS

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Abstract: We studied duck nest success and predator community composition in relation to size of discrete patches of nesting cover in the Prairie Pothole Region (PPR) of the United States in 1993–95. We focused on nests in uplands that were seeded to perennial grasses and forbs and enrolled in the Conservation Reserve Program (CRP) in Minnesota, North Dakota, and South Dakota. We estimated daily survival rates (DSRs) of upland duck nests and indices of activity for red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), striped skunks (*Mephitis mephitis*), and Franklin's ground squirrels (*Spermophilus franklinii*), and related these variables to habitat patch size. The effect of patch size (small vs. large) on estimated annual mean DSR was dependent on date of nest initiation (early vs. late) and year. Examination of within-year comparisons for early and late nests suggested that DSR was generally greater in larger habitat patches. Activity indices for the 5 mammalian nest predators were influenced differently by year, location, and patch size. Activity indices of the red fox were greatest in small patches. Coyote indices were the most inconsistent, demonstrating a year × location × patch size interaction. Activity indices of the striped skunk and American badger varied only among years. Franklin's ground squirrel indices were affected by study area location, with higher indices in the southeast than the northwest. Red fox activity was weakly correlated with that of the striped skunk and coyote. Although a positive relationship between habitat patch size and nest success probably exists, we believe the experiment to fully test this hypothesis will continue to be elusive.

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Key words: Conservation Reserve Program, habitat patch size, mammalian predators, nest success, Prairie Pothole Region, upland-nesting ducks.

Landscapes in the PPR of the United States and Canada have been altered extensively due to drainage of wetlands and conversion of native grasslands to annually tilled cropland (Higgins 1977, Sugden and Beyersbergen 1984, Greenwood et al. 1995, Miller and Nudds 1996). This region is a primary breeding ground for many waterfowl species (Bellrose 1980, Batt et al. 1989), and many landscape changes have been detrimental to North American duck populations. Managers have targeted the PPR for preservation and restoration of wetland and upland habitats vital to duck populations (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986).

Grassland-nesting ducks require secure upland habitats for nesting and productive wetland habitats for foraging. Wetland features largely determine settling patterns of ducks on their breeding grounds (Johnson and Grier 1988), suggesting that ducks select breeding areas based on nutritional requisites rather than nest security. Although prior nest success may affect homing to breeding areas (Lokemoen et al. 1990), many ducks settle in landscapes where upland nesting habitat is sparse and nest predation rates are high (Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995). Thus, in areas attractive to ducks, managers need to provide secure nesting habitats. Moreover, be-

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cause predation is a major factor affecting nest success, composition of the predator community also should be considered in the context of habitat requirements for nesting ducks (Greenwood 1986, Johnson et al. 1989, Sovada et al. 1995).

Clark and Nudds (1991) challenged waterfowl biologists to examine relationships among habitat patch size and composition, and duck nest success in order to guide management efforts to preserve or restore nesting habitats. We attempted to do this by focusing on land enrolled in the CRP (Young and Osborn 1990). Beginning in 1985, much cropland in the United States' portion of the PPR was restored to perennial grasslands through the CRP. When we initiated the present study in 1993, about 2.5 million ha were enrolled in CRP in Minnesota, Montana, North Dakota, and South Dakota (Kantrud 1993). Fields enrolled were of various sizes and widely dispersed. Our objectives were to (1) estimate DSRs of duck nests in discrete habitat patches of nesting cover of different sizes, (2) determine the composition of predator communities associated with these habitat patches, and (3) examine the relation of patch size to predator community composition and DSRs of duck nests.

STUDY LOCATION

We conducted our study in a portion of the PPR of Minnesota, North Dakota, and South Dakota during 1993–95. Topography ranged from gently undulating to rolling. This study required discrete patches of perennial grassland. A preliminary survey of candidate areas in the Missouri Coteau, which is approximately the same area as the Great Plains portion of the PPR (Fig.1; Stewart 1975:6, Bluemle 1991), revealed that perennial grassland in the Missouri Coteau often composed >30% of the landscapes (R. J. Greenwood, Northern Prairie Wildlife Research Center, unpublished data). In such landscapes, where areas of perennial grassland were nearly continuous, we often were unable to identify discrete patches of grassland. Necessarily, our study was conducted in localities where <30–35% of the landscape was composed of perennial grassland. Most locations were in the Central Lowlands portion of the PPR; few were in the Great Plains (Fig. 1). Areas we selected contained uplands that were largely cultivated annually for crops; primarily corn and soybeans in the east, changing to small grains in the west. Untilled uplands were pastures, haylands, and idle grasslands; much of the idle grassland was enrolled in the CRP.

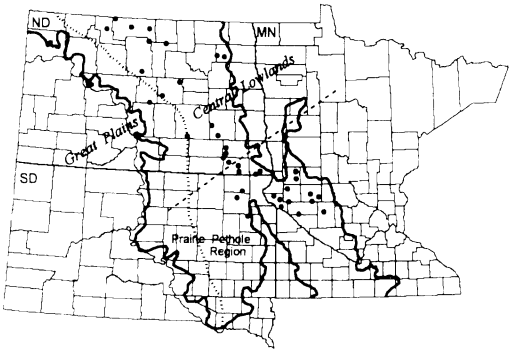

Fig. 1. Location of areas studied (solid dots) in the Prairie Pothole Region (solid line) of Minnesota, North Dakota, and South Dakota, 1993–95. Dashed line separates the Great Plains and Central Lowlands physiographic regions (after Kantrud 1993). Diagonal dashed line separates study sites by median patch location (northwest or southeast of 46°8'N and 97°43'W).

METHODS

Study Area Criteria

We selected candidate study areas from approximately 500 potential study sites (10.4 km^2 each) that represented a stratified random sample of townships with high management potential for duck production (Cowardin et al. 1995). Landscapes of these sites had been delineated previously by class of upland habitat (Cowardin et al. 1988, Reynolds et al. 1994) or wetland type (Cowardin et al. 1979). Initially, we identified potential study sites that contained ≥16 ha of CRP and sufficient ponds to attract ≥2 pairs/km^2 of breeding mallards (*Anas platyrhynchos*), based on a pairs/wetland regression model (Reynolds et al. 1996) or prior ocular counts by the U.S. Fish and Wildlife Service. Sites that satisfied these criteria became candidate study areas. For each candidate area, we expanded habitat coverage 1.6 km in each cardinal direction, based on information obtained from local Natural Resources Conservation Service offices and using geographic information system (GIS) mapping techniques. All habitats in the resulting 141 41.4-km^2 areas were then allocated to 4 new classes: (1) Perennial Cover (grassland, hayland, planted wildlife cover, woodland, and CRP land), (2) Cropland, (3) Farmstead (feedlots, towns, and recreation areas), and (4) Wetland. Landscape features clas-

sified as odd area or right-of-way (Cowardin et al. 1988) were included in adjacent habitats.

Using the new habitat classification, we delineated habitat patches of nesting cover in each 41.4-km^2 candidate area by consolidating contiguous tracts of Perennial Cover (Fig. 2) and estimated the size of each patch. To be contiguous, tracts needed to share ≥1 side (i.e., tracts meeting only at a corner in a checkerboard fashion were not considered contiguous). Because we included road right-of-way in adjacent habitats, tracts separated only by a road were considered contiguous. Narrow linear extensions (approximate length:width ratio ≥4:1) of tracts of Perennial Cover were excluded from patches. Rivers and irrigation canals that may restrict movements of some mammalian predators of duck nests were considered sufficient to divide contiguous areas of Perennial Cover into separate patches. Temporary and seasonal wetland basins were included in patch size totals, and semipermanent and permanent wetland basins and riparian wetlands (Cowardin et al. 1979) were excluded.

To qualify as a study area, a candidate area had to contain ≥2 different-sized patches, each containing ≥4 ha of land enrolled in the CRP. We recognized 3 different patch-size categories: ≤32 ha, 33–130 ha, and >130 ha. This criterion ensured that each study area would have a wide range of patch sizes. Forty-seven candidate areas satisfied all criteria for a study area.

In the final step of study area selection, we annually grouped (4 groups) the remaining candidate areas by locality for logistical convenience, each locality encompassing about 26,000 km^2. Grouping provided broad geographic representation without imparting prior knowledge of factors likely to affect nest survival rates; this also allowed us to efficiently deploy field crews. Within a group, we annually selected 6 study areas that were ≥8 km apart, using random methods when >6 were available. In 1993, we selected study areas from west-central Minnesota, southeastern North Dakota, and northeastern South Dakota. We excluded central and north-central North Dakota that year because most wetlands from those parts of the state were dry due to severe drought (Kantrud 1993, Todhunter 1995). In 1994 and 1995, we expanded the scope of our study in North Dakota after abundant precipitation (National Oceanic and Atmospheric Administration 1993,

Table 1. Characteristics of small or large habitat patches[a] studied in the Prairie Pothole Region of North Dakota, South Dakota, and Minnesota, 1993–95.

	1993				1994				1995			
	Small $n = 32$		Large $n = 35$		Small $n = 36$		Large $n = 35$		Small $n = 37$		Large $n = 37$	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Perennial cover (ha)	36	6–101	578	107–1,789	48	5–101	593	106–2,342	48	4–101	588	106–2,342
% CRP	86		49		82		46		84		48	
% hayland	2		5		4		4		4		4	
% grassland	10		41		12		47		11		45	
% woodland	2		5		2		3		2		3	
Wetland[b] (ha)	7	0–105	155	1–596	12	0–118	121	4–468	11	0–118	118	4–468
Area past perimeter[c] (ha)	32		131	2–311	35	26–42	117	11–287	33	26–40	117	7–287

[a] Patch was composed of all adjoining tracts of Perennial Cover (grassland, hayland, planted cover, woodland, and land enrolled in the Conservation Reserve Program) that shared a common side, and temporary and seasonal wetlands located within the Perennial Cover. Patch size based on area of Perennial Cover: small patch = ≤105 ha, large patch >105 ha.

[b] Includes only seasonal and temporary basins within Perennial Cover.

[c] Study area was 41.4 km^2. Area of Perennial Cover contiguous with patches that abutted the perimeter of a study area was estimated to a distance of 0.8 km from perimeter. Number of patches beyond perimeter for small and large patches respectively, was 1 and 24 in 1993, 4 and 28 in 1994, and 3 and 30 in 1995.

Table 2. Results of analysis of variance on daily survival rates of upland duck nests in the Prairie Pothole Region of Minnesota, North Dakota, and South Dakota in relation to patch size[a], location (northwest or southeast of 46°8′N and 97°43′W), nest initiation date[b] (early or late), and year (1993, 1994, or 1995).

Source	df	*F*	*P*
Patch size	1,80	4.46	0.038
Location	1,80	0.39	0.536
Patch size × location	1,80	3.02	0.086
Initiation date	1,100	5.22	0.024
Initiation date × location	1,100	1.52	0.221
Initiation date × patch size	1,100	0.14	0.714
Initiation date × patch size × location	1,100	0.02	0.902
Yr	2,80	2.01	0.140
Yr × patch size	2,80	0.07	0.936
Yr × location	2,80	0.45	0.639
Yr × patch size × location	2,80	0.59	0.556
Yr × initiation date	2,58	3.79	0.028
Yr × initiation date × patch size	2,58	3.37	0.041
Yr × initiation date × location	2,58	1.03	0.362
Yr × initiation date × patch size × location	2,58	1.22	0.302

[a] Patch defined as in Table 1.
[b] Early and late nests were partitioned by median nest initiation date each year. Early nests were initiated on or before 1 June in 1993, and 7 June in 1994 and 1995; late nests were initiated after those dates.

1994) filled wetland basins and promoted growth of lush vegetation in uplands.

Patch Selection

Our goal was to search approximately 162 ha of CRP for nests in each study area. We allocated our search effort in each area based on patch size. We anticipated DSR estimates in patches ≤32 ha would be imprecise due to few nests; therefore in each study area, we selected all available patches of this size and designated all CRP land in these patches to be searched for nests. In patches >32 ha, where we anticipated more precise DSR estimates due to a larger number of nests, we divided CRP land into ≤32-ha tracts (Fig. 2) and systematically sampled these until we had searched ≥25% of the CRP land in the patch. We used systematic sampling because it distributed the sample of nests throughout the patch. If >1 patch of >32 ha was available in a study area, we randomly selected 1 patch of each size (>32–130 ha and >130 ha) to be searched when each category of patch size was represented in the study area. Lastly, we contacted landowners or tenants of all selected patches to obtain permission to conduct the study. If permission was denied to the extent that we believed we could not adequately sample CRP land in a patch, we selected a replacement patch in the same study area. If a replacement patch was unavailable in that study area, we abandoned the area and started the selection process over in the nearest qualified study area.

Table 3. Numbers of nests, exposure days, and least-squares means estimates of daily survival rate of upland duck nests in the Prairie Pothold Region of Minnesota, North Dakota, and South Dakota relative to year × nest initiation date[a] (early or late) × patch size[b] interaction ($F_{2,49}$ = 5.86, P < 0.01). Within categories early or late for each year, statistical differences (*) between patch sizes are based on Fisher's protected LSD procedure ($P \leq 0.05$).

		Number of nests		Exposure days		Daily survival rate			
						Early		Late	
Yr	Patch size	Early	Late	Early	Late	Estimate	SE	Estimate	SE
1993	Small	79	116	849	1,444	0.924	0.014	0.943	0.010
	Large	294	248	3,515	3,181	0.937	0.008	0.950	0.007
1994	Small	174	151	2,162	3,467	0.930	0.007	0.949	0.007
	Large	289	280	2,051	3,468	0.944	0.006	0.954	0.006
1995	Small	231	231	3,028	5,080	0.950	0.006	0.937*	0.006
	Large	400	380	2,554	4,920	0.952	0.006	0.962*	0.006

[a] Early and late nest initiation dates defined as in Table 2.
[b] Patch defined as in Table 1.

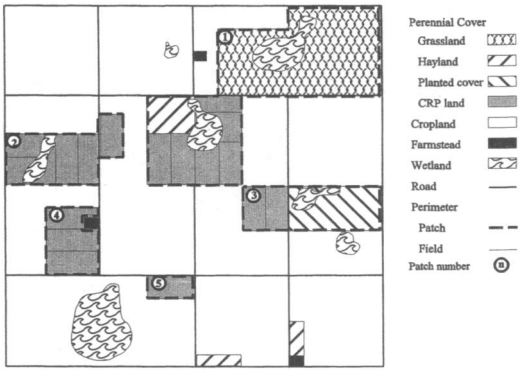

Fig. 2. Schematic diagram of a 41.4-km² (16-mi²) study area containing 5 patches.

Habitat Composition

We updated our habitat estimates for selected study areas each year based on current (summer 1993 or 1994) color infrared aerial photography (1:20,000) verified by ground surveillance. Upland habitat (Cropland, Perennial Cover, Farmstead) polygons were delineated and data were digitized using Map and Image Processing System software (MicroImages 1992). Wetland-habitat data in digital format were obtained from the National Wetlands Inventory (U.S. Fish and Wildlife Service, St. Petersburg, Florida, USA), and merged with digital files of upland habitat. For each study area, we used merged data to create a final habitat map and text file containing area and perimeter measurements of each polygon.

In some instances, ground surveillance revealed patches that abutted and extended beyond the perimeter of a 41-km² study area. Functionally, these patches were larger than our initial measurements portrayed. For such patches, we estimated the area of Perennial Cover for an additional 0.8 km beyond the patch, and used these larger estimates of patch size in our analyses.

Collection of Nest Data

We searched CRP land for duck nests 3 times annually using vehicle-towed chain drags and procedures similar to those described by Higgins et al. (1969). A nest was defined as ≥1 egg tended by a female when found. Searches began approximately the first week of May, fourth week of May, and second week of June, and were conducted daily between 0700 and 1400 hr. Standard procedures described by Klett et al. (1986) were followed for marking nests, re-

Table 4. Results of analysis of variance on predator activity indices in the Prairie Pothole Region in Minnesota, North Dakota, and South Dakota in relation to patch size[a], location (northwest or southeast of 46°8'N and 97°43'W), and year (1993, 1994, 1995).

Source	df	Red fox		Coyote		Striped skunk		American badger		Franklin's ground squirrel	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Patch size	1,117	4.11	0.045	1.88	0.173	0.49	0.485	0.01	0.909	0.02	0.886
Location	1,117	0.01	0.906	4.49	0.036	1.09	0.300	1.48	0.226	14.78	<0.001
Patch size × location	1,117	0.52	0.470	0.03	0.862	0.34	0.560	0.46	0.500	0.30	0.587
Yr	2,81	2.24	0.113	4.93	0.010	17.38	<0.001	6.44	0.003	2.82	0.066
Yr × patch size	2,81	2.05	0.135	0.20	0.817	0.16	0.853	0.67	0.693	0.65	0.527
Yr × location	2,81	5.33	0.007	0.12	0.891	0.36	0.701	0.78	0.463	0.07	0.929
Yr × patch size × location	2,81	0.37	0.691	4.07	0.021	1.31	0.276	1.49	0.232	0.85	0.431

[a] Patch defined as in Table 1.

Table 5. Correlation coefficients between daily survival rates[a] (DSR) of upland duck nests in the Prairie Pothole Region of Minnesota, North Dakota, and South Dakota, and between explanatory variables, 1993–95.

	n[b]	DSR (late)[c]	Patch location[d]	Patch size[e]	Activity index[f]					
					Red fox	Coyote	Striped skunk	American badger	Franklin's ground squirrel
DSR (early)	184	0.03	0.05	0.15	−0.06	0.21	0.02	−0.06	−0.01
DSR (late)	182		0.02	0.19	−0.16	0.05	0.07	−0.07	−0.04
Patch location	212			0.13	−0.02	0.14	0.02	−0.12	−0.30
Patch size	212				−0.22	0.12	−0.07	−0.03	−0.01
Red fox	212					−0.15	0.29	0.16	−0.03
Coyote	212						0.21	0.08	0.12
Striped skunk	212							0.06	−0.01
American badger	212								0.18

[a] Estimated by Mayfield method, as modified by Johnson (1979).
[b] Number of patch × year combinations; n = 154 for correlation of DSR (early) × DSR (late).
[c] Early and late nest initiation dates defined as in Table 2.
[d] Patch defined as in Table 1.
[e] Patch size = ln (ha).
[f] Mean proportion of plots around study fields that contained carnivore tracks during 3 annual surveys, or number of unique Franklin's ground squirrels captured per trap day in 4 24-hr periods (Sargeant et al. 1993, Sovada et al. 1995).

cording locations, and documenting data when nests were found and revisited. Nests were revisited at about 21-day intervals until the nest was successful (≥1 egg hatched), the clutch was destroyed, or the nest was abandoned by the hen. Abandonment was attributed to investigator influence if a nest appeared to have been abandoned on day of discovery. For nests abandoned after ≥1 egg was destroyed or missing, we attributed abandonment to predator influence. Nest fate was classified as unknown if a nest was not relocated.

Estimation of Predator Activity Indices

We conducted systematic surveys for tracks of coyotes, red foxes, American badgers, and striped skunks using methods similar to Sargeant et al. (1993) and Sovada et al. (1995). Three surveys (early May, early Jun, and late Jun) were conducted annually in 50- × 50-m grid-plots laid out along the entire perimeter of each CRP tract that we searched for duck nests. Within each grid-plot, personnel looked for tracks in naturally occurring sites with soil suitable for track deposition. Suitability of soil condition, length of track acquisition period, and number of potential sites for tracks were rated in each plot at time of each survey (Sargeant et al. 1993). The number of grid-plots depended on the size of the CRP tract; grid-plots that contained no sites with potential for observing tracks were excluded. Results of the 3 surveys in a patch were combined annually for each species; data from small patches were insufficient for partitioning the data into early and late periods. We excluded a patch if <20 total grid-plots were rated as good for registering tracks. For each species, the activity index in a patch was the percent of the usable grid-plots with suitable soil conditions that contained tracks of that species.

We conducted systematic live-trap surveys for Franklin's ground squirrels during 5 days in early July (Sargeant et al. 1993) in each CRP tract in which we searched for duck nests. Trap sites (6 per tract of CRP ≤20 ha, 9 per tract 21–40 ha, or 12 per tract >40 ha) were randomly selected from a pool of sites in each tract considered to be best (e.g., dense grass, brush, or rock pile) for Franklin's ground squirrels. Traps (6 × 6 × 19 cm) baited with canned sardines and bacon pieces were set for 4 24-hr periods and checked at the end of each period. Captured animals were uniquely marked with a small spot

of paint on their back to permit identification and immediately released at the capture location. The activity index in a patch for Franklin's ground squirrels was the capture rate, expressed as number of unique individuals captured per trap day (1 trap set for a 24-hr period).

Data Analysis

We estimated the DSR of duck nests for each patch within each year and study area using the Mayfield method as modified by Johnson (1979). Nests of all species were pooled within each patch and year to increase precision of estimates. Nests that showed evidence of egg depredation when discovered or that were abandoned due to investigator influence were excluded from analyses.

We assessed the effect of patch size, patch location, nest initiation date, and year on DSR estimates using analysis of variance (ANOVA) techniques. For analyses, patches were partitioned into 2 size categories: those above and those below the median sized area of perennial cover for all patches (hereafter, small patches and large patches). Partitioning patches into >2 categories would have sacrificed precision of estimates on the smaller patch-size category. Because geographic location may influence DSR (Klett et al. 1988) as well as the predator community (Sargeant et al. 1993), we partitioned patches into a northwest or southeast location, based on median study area location. Study areas were situated along a northwest to southeast gradient (Fig. 1). Latitude of study areas was highly correlated with longitude ($r = -0.88$), so we derived a single term (hereafter, location) to describe each study area, based on the first component in a principal components analysis (PCA; Johnson and Wichern 1988). We accomplished the PCA using PROC PRINCOMP (SAS Institute 1989). The first principal component accounted for 94% of the variation between latitude and longitude. Nest initiation date also may influence DSR (Johnson et al. 1989, Greenwood et al. 1995), so we included date in the ANOVA. We estimated the date each nest was initiated by counting back from the date it was found, 1 day for each egg in the clutch and 1day for each day of incubation minus 1. Nests were partitioned into early nests and late nests by the median date that nests were initiated each year (Greenwood et al. 1995); early nests were initiated on or before the median date and late nests were initiated after the median date. Partitioning nests in the ANOVA by median date reduced the chances of violating Mayfield's assumption of constant DSRs. Further partitioning of nests would have sacrificed precision of DSR estimates on the smaller patches. We did not account for study area in the ANOVA because our method of sampling patches and use of the first principal component to describe their locations resulted in a relatively uniform distribution of small and large patches throughout the region of our study.

We conducted the ANOVA to examine DSR using a mixed general linear model procedure (PROC MIXED; SAS Institute 1997). The model was of a strip-plot form with repeated measures (Milliken and Johnson 1984, Littell et al. 1996). Patch was the random whole unit within patch size (small or large) and location (northwest or southeast). The date nests were initiated (early or late) was considered a subunit within patch. Year was a repeated measure on each patch. Because precision of DSR estimates is proportional to exposure days (Johnson 1979), we weighted by exposure days in the ANOVA. Mean differences for significant main effects and interactions were isolated using Fisher's protected least significant difference procedure (Milliken and Johnson 1984). We did not attempt to model the variance–covariance of year or spatial relationships among patches, because our initial examination indicated DSRs were as likely to increase, decrease, or remain the same from year-to-year and from patch-to-patch, regardless of patch size or location. We did not include predator indices as covariates in the mixed model because preliminary analyses indicated that predator indices varied significantly with our treatments (i.e., patch size, year, location).

We conducted ANOVAs to assess effects of patch size, patch location, and year on predator activity indices using a similar model to that described above, but without date. Because the precision of the predator-index estimate is proportional to the number of grid-plots, we weighted by number of grid-plots in the ANOVA.

Because we could not simultaneously examine the influence of both patch size and predator activity on DSRs, we explored those relationships using correlation analysis. We calculated simple correlations among DSRs of early or late nests, patch size, location, and indices to

activity of coyotes, red foxes, American badgers, striped skunks, and Franklin's ground squirrels measured on each patch. Patch size, location, and predator indices were entered as continuous variables; we transformed patch size to its natural logarithm. Each patch by year was considered to be an independent observation. We considered only correlation coefficients >|0.10|, because we wished to eliminate effects due merely to large sample sizes.

RESULTS

We worked on 24 study areas annually, 1993–95. There were 38 unique study areas, and some were sampled in multiple years: 14 areas for 1 year, 14 areas for 2 years, and 10 areas for 3 years. Percent composition of our study areas was 58 ± 2% Cropland ($\bar{x}$ ± SE), 28 ± 2% Perennial Cover, 13 ± 1% Wetland, and 1 ± 0.2% Farmstead. We studied 212 patch × year combinations, with patches ranging in size from 5 to 2,810 ha (Table 1); the median area of Perennial Cover for all patches was 105 ha. The number of patch × year combinations sampled by year was 67 in 1993, 71 in 1994, and 74 in 1995 (Table 1). Of the 212 combinations, 54 were studied in 1 year, 43 in 2 years, and 24 in all 3 years. The median patch location was 46°8′N and 97°43′W, which is near the center of Ransom County, North Dakota. Area of wetland in patches ranged from 0 to 596 ha. Maximum mean proportion of CRP land in studied patches ranged from 86% in small patches to 49% in large patches. Maximum mean proportion of grassland ranged from 12% in small patches to 47% in large patches. In all years, mean proportion of hayland and woodland in patches was ≤5% each. The CRP land was seeded mostly to introduced grasses and legumes: wheatgrasses (*Agropyron* spp.), alfalfa (*Medicago sativa*), or sweet clover (*Melilotus* spp.), and sometimes smooth brome (*Bromus inermis*; J. Clapper, National Resource Conservation Service, Jamestown, North Dakota, personal communication). Fields we studied had been enrolled in the CRP since before 1990, thus vegetation had been established for 3–4 years before our study.

We found 2,940 duck nests; 2,873 nests met the criteria for inclusion in analyses. Species composition of the nests was 46% blue-winged teal (*Anas discors*), 23% mallard, 16% gadwall (*A. strepera*), 7% northern shoveler (*A. clypeata*), 7% northern pintail (*A. acuta*), and 1% (combined) American wigeon (*A. americana*), green-winged teal (*A. crecca*), redhead (*Aythya americana*), and lesser scaup (*A. affinis*). Estimates of DSR for patches varied from 0.714 to 1.000, with exposure days in patches ranging from 1 to 1,213. Median nest initiation dates were 1 June in 1993, and 7 June in 1994 and 1995.

The effect of patch size on estimates of mean DSR depended on year and whether the nest was initiated early or late in the season (Table 2). Estimated DSRs were significantly greater for nests found in large patches than small patches ($P < 0.05$) in 1 of the 6 possible 2-way comparisons, and the trend was similar for the remaining 5 comparisons (Table 3).

Activity indices for the 5 mammalian nest predators that we surveyed were influenced differently by year, location, and patch size (Table 4). Indices of red fox were affected by patch size ($F_{1,117} = 4.11$, $P = 0.045$), with greater indices in small patches than in large patches. The relationship between red fox indices and location depended on year ($F_{1,117} = 5.33$, $P = 0.007$), and were higher in the northwest than the southeast in 1994 ($P = 0.02$). In contrast, coyote indices were inconsistent with a significant year × location × patch size interaction ($F_{1,81} = 4.07$, $P = 0.021$). Striped skunk and American badger indices varied only among years ($F_{1,81} = 17.38$, $P < 0.001$, and $F_{1,81} = 6.44$, $P = 0.003$, respectively), with indices for both species increasing from 1993 to 1995. Franklin's ground squirrel indices were affected by location ($F_{1,117} = 14.78$, $P < 0.001$), with higher indices in the southeast than the northwest. Year also had a marginal affect ($F_{1,81} = 2.82$, $P = 0.066$) on ground squirrel indices, with indices increasing from 1993 to 1995. Despite their variability, mean indices for all surveyed predators were generally highest in 1995.

We detected weak correlations between DSR estimates and several explanatory variables; some of the explanatory variables themselves covaried (Table 5). Strongest correlations were a negative relation between patch location and activity indices of Franklin's ground squirrels ($r = -0.30$), and a positive relation between activity indices of striped skunks and both red foxes and coyotes ($r = 0.29$ and $r = 0.21$, respectively). The DSRs of both early and late nests were positively correlated with patch size ($r = 0.15$ and $r = 0.19$, respectively). Surprisingly, we detected only a weak positive correlation (r

= 0.03) between DSRs of early and late nests, suggesting that factors influencing nest success may change within nesting seasons, or be obscured by sampling error. The DSRs of early nests were positively correlated with indices of coyote activity ($r = 0.21$) and DSRs of late nests were negatively correlated with indices of red fox activity ($r = -0.16$). Indices of coyote activity ($r = 0.13$) and patch size ($r = 0.14$) increased from southeast to northwest. Patch location was negatively correlated with indices of American badger activity ($r = -0.12$), which was positively correlated with indices of both red fox ($r = 0.16$) and Franklin's ground squirrel ($r = 0.18$). Red fox activity indices were negatively correlated with indices of coyote activity ($r = -0.15$).

DISCUSSION

Our study did not clearly explain the relations between patch size and factors that affected DSRs of duck nests. Although we found that mean DSR tended to be lower in small patches compared to large patches, success also depended on nest initiation date and year of study. Our ability to explain factors that affected nest success was influenced by high variability in our DSR estimates for each patch. This high variability was not entirely unexpected, however, because duck production in the PPR is affected by numerous environmental factors (Greenwood et al. 1995). Variability might have been affected by our pooling of nests to compensate for small samples, if DSRs differed among species. However, Greenwood et al. (1995), with a much larger sample of nests than ours, observed no difference in DSRs among prairie nesting duck species in habitats similar to those we studied. Even if slight variation should occur in DSRs among species, the robustness of the Mayfield method renders it most appropriate and estimates will not be misleading (Klett and Johnson 1982). Williams (1997) suggested that environmental variation, which influences biological processes and induces stochasticity in population dynamics, is the most recognizable component of uncertainty in waterfowl management.

During our study, the PPR experienced a period of rapid transition from extreme drought to extreme wet conditions, which likely affected our findings. This transition gave rise to possibly the best conditions for breeding waterfowl in the PPR in recent times (Krapu 1994, U.S. Fish and Wildlife Service and Canadian Wildlife Service 1995). Besides the obvious changes in wetland and upland habitats associated with this transition, populations of some mammalian predators and their prey species also responded positively to conditions brought on by abundant precipitation (Greenwood and Sovada 1996, Greenwood et al. 1998). In addition to weather-induced factors, other factors affecting predator populations may have influenced our study findings. For instance, striped skunk populations were reduced sharply by rabies in some localities, an occurrence that is probably more common than previously recognized (Greenwood et al. 1997), as rabies is enzootic in striped skunks in prairie regions (Charlton et al. 1991). Likewise, an outbreak of sarcoptic mange (*Sarcoptes scabiei*) affected coyote and red fox numbers and distribution in North Dakota and Minnesota during study years (S. Allen, North Dakota Game and Fish Department, Bismarck, personal communication as cited in Greenwood and Sovada [1996]).

Red foxes, which are important predators of nesting ducks (Sargeant 1972, Sargeant et al. 1984, Johnson et al. 1989), had activity indices that tended to be negatively correlated with patch size and coyote indices. This suggests that, in larger patches where coyotes tended to have higher activity indices, the effect of red foxes on nest survival may have been mediated by presence of coyotes. Sovada et al. (1995) found a similar affect on nest success where coyotes were present. Coyotes are known to displace red foxes (Voigt and Earle 1983, Sargeant et al. 1987*a*). Red fox indices also tended to be positively correlated with striped skunk indices, suggesting that these species occur together. A similar relationship between red foxes and striped skunks was reported by Johnson et al. (1989) in Canadian prairies. Striped skunks also are important predators on duck eggs (Greenwood 1986, Johnson et al. 1989), thus their effect may have been additive to the effect of red foxes in small patches. The Franklin's ground squirrel is another important predator on duck eggs (Sargeant et al. 1987*b*). Our finding that Franklin's ground squirrels were more common in southeastern than northwestern locations is consistent with knowledge of their distribution in the PPR (Sargeant et al. 1993).

Kantrud (1993) reported lower success in southeastern North Dakota among ducks nesting in small ($\bar{x}$ = 32 ha) fields of planted nesting

cover than in nearby larger ($\bar{x}$ = 64 ha) CRP fields. Greenwood et al. (1987) observed that nest success of ducks in Canadian prairies was positively correlated with amount of grassland in the landscape, but did not test for effects of patch size. Burger et al. (1994) and Winter (1998) observed a similar trend toward lower survival rates for nests in smaller patches than in larger patches based on artificial nests, however, these findings are not directly comparable with ours (Clark and Wobeser 1997, Guyn and Clark 1997).

MANAGEMENT IMPLICATIONS

Although we were unable to identify patch characteristics or qualities that would ensure nest success above threshold levels for prairie ducks (Cowardin et al. 1985, Klett et al. 1988), our findings suggest that there is a positive relationship between patch size and nest success. We concur with Clark and Nudds (1991), however, that it may be impractical to conduct the experiment needed to overcome inherent environmental variation, and thus, to convincingly test this hypothesis. Our study, using available techniques and existing CRP fields, employed a rigorous analytical survey design that was replicated across the landscape of the PPR of 3 states during a 3–year period of optimum conditions for breeding ducks and record high duck production in the PPR (Reynolds et al. 1994). It is difficult to imagine a period when a better distributed sample of nests could be obtained over as extensive an area. Our results suggest that landscapes with sufficient wetlands and ample grassland configured in relatively large tracts are the most productive areas for nesting ducks. This is consistent with findings of Greenwood et al. (1995), who evaluated nest success throughout a large portion of the PPR in Canada. The most appropriate size, configuration, and location of preserved and restored tracts of grassland to be of greatest benefit to duck populations is the subject of much conjecture (Clark and Nudds 1991). We believe it is sufficiently clear, however, that small isolated tracts of nesting habitat are of marginal benefit to nesting ducks, unless concerted efforts are made to manage these tracts to reduce predator effects. Small isolated tracts of grassland tend to be visited extensively by numerous predators of nesting ducks, especially red foxes. Restoration of small isolated tracts of grassland habitat without accompanying predator management may have negative affect on duck populations, because females will be attracted to areas where there they likely will be exposed to high levels of predation.

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