1995

Factors Associated With Duck Nest Success in the Prairie Pothole Region of Canada

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WILDLIFE MONOGRAPHS

(ISSN:0084-0173)

A Publication of The Wildlife Society

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by

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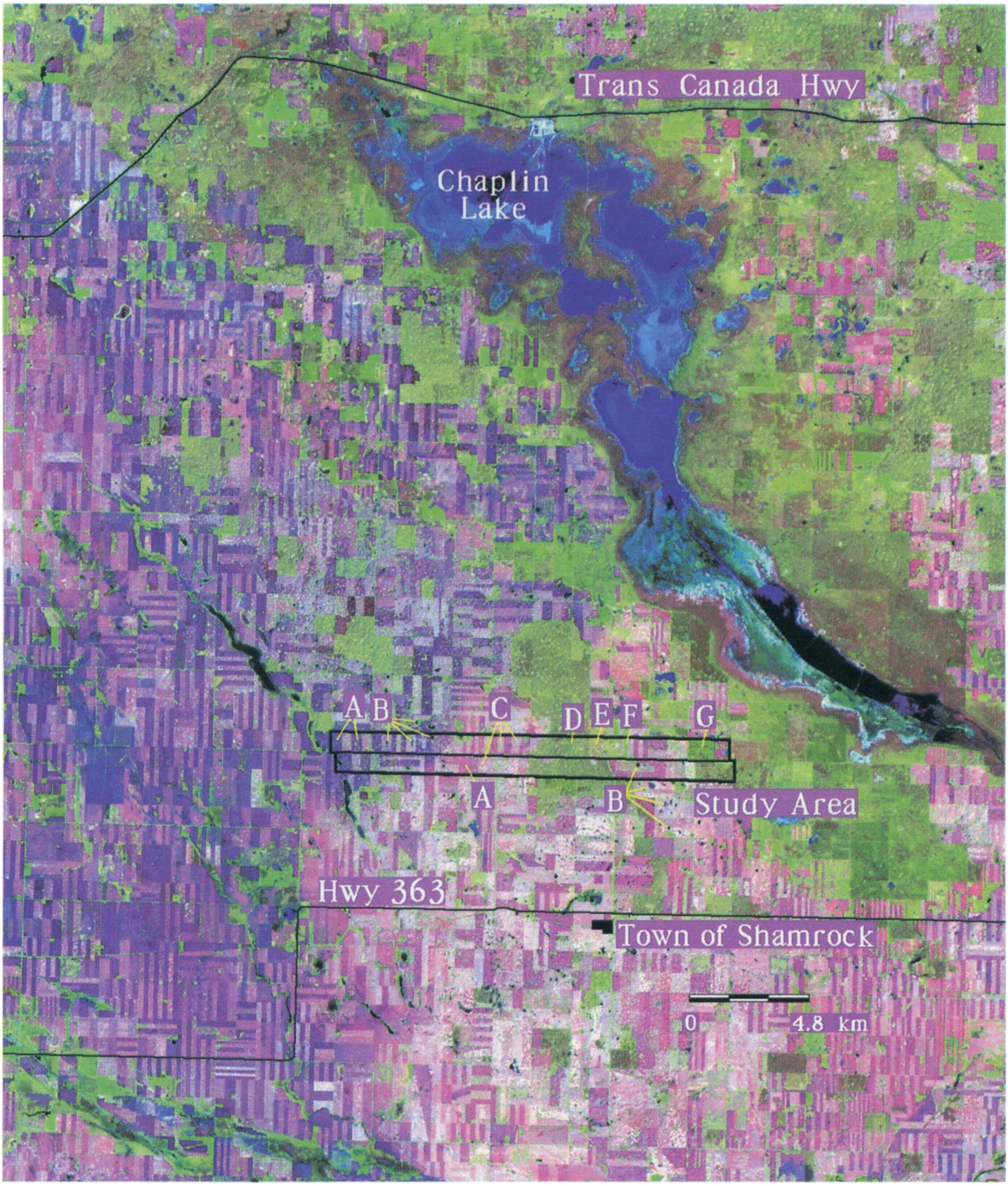
NO. 128 **JANUARY 1995**



FRONTISPIECE. Missouri Coteau in southern Saskatchewan, showing fragmented habitats and 25.6-km^2 Shamrock Study Area. Labeled habitats are (A) fallow field, (B) wet wetland, (C) stubble field, (D) native grassland, (E) seeded grassland, (F) fall-seeded grainfield, and (G) alfalfa field. Upper left corner of image is located at 50°30′3.4″N latitude, 106°59′17.4″W longitude; lower right corner is at 50°3′52.0″latitude, 106°22′59.6″ longitude. Produced from 21 May 1991 Landsat-5 Thematic Mapper image; bands 5 (1.55–1.75 μm), 4 (0.76–0.90 μm), and 3 (0.63–0.69 μm) displayed through red, green, and blue filters, respectively.

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Abstract: Populations of some dabbling ducks have declined sharply in recent decades and information is needed to understand reasons for this. During 1982–85, we studied duck nesting for 1–4 years in 17 1.6 by 16.0-km, high-density duck areas in the Prairie Pothole Region (PPR) of Canada, 9 in parkland and 8 in prairie. We estimated nest-initiation dates, habitat preferences, nest success, and nest fates for mallards (*Anas platyrhynchos*), gadwalls (*A. strepera*), blue-winged teals (*A. discors*), northern shovelers (*A. clypeata*), and northern pintails (*A. acuta*). We also examined the relation of mallard production to geographic and temporal variation in wetlands, breeding populations, nesting effort, and hatch rate.

Average periods of nest initiation were similar for mallards and northern pintails, and nearly twice as long as those of gadwalls, blue-winged teals, and northern shovelers. Median date of nest initiation was related to presence of wet wetlands (contained visible standing water), spring precipitation, and May temperature. Length of initiation period was related to presence of wet wetlands and precipitation in May, June temperature, and nest success; it was negatively related overall to drought that prevailed over much of Prairie Canada during the study, especially in 1984.

Mallards, gadwalls, and northern pintails nested most often in brush in native grassland, blue-winged teals in road rights-of-way, and northern shovelers in hayfields and small (<2 ha) untilled tracts of upland habitat (hereafter called Odd area). Among 8 habitat classes that composed all suitable nesting habitat of each study area, nest success estimates averaged 25% in Woodland, 19% in Brush, 18% in Hayland, 16% in Wetland, 15% in Grass, 11% in Odd area, 8% in Right-of-way, and 2% in Cropland. We detected no significant difference in nest success among species: mallard (11%), gadwall (14%), blue-winged teal (15%), northern shoveler (12%), and northern pintail (7%). Annual nest success (pooled by study area and averaged [unweighted] over all study areas) was 17% in 1982, 15% in 1983, 7% in 1984, and 14% in 1985.

We estimated that predators destroyed 72% of mallard, gadwall, blue-winged teal, and northern shoveler nests and 65% of northern pintail nests. In prairie, average nest success decreased about 4 percentage points for every 10 percentage points increase in Cropland, suggesting that under conditions of 1982–85, local populations of these species probably were not stable when Cropland exceeded about 56% of available habitat. We found recent remains of 573 dead ducks during 1983–85; most were females (*Anas* spp.) apparently killed by predators. In some years, mallards and northern pintails were more numerous among dead ducks than we expected. More females than males were found dead among mallards and northern shovelers, suggesting higher vulnerability of females. Of factors we examined, nest-success rate appeared to be the most influential factor in determining mallard production. Nest success varied both geographically and annually.

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Key words: *Anas acuta, A. clypeata, A. discors, A. platyrhynchos, A. strepera,* blue-winged teal, Canada, dabbling ducks, gadwall, mallard, nest success, northern pintail, northern shoveler, Prairie Pothole Region.

CONTENTS

INTRODUCTION

Populations of several species of dabbling ducks have declined in recent decades in North America. In the early 1980's, mallard (*Anas platyrhynchos*), blue-winged teal (*A. discors*), and northern pintail (*A. acuta*) breeding populations were near their lowest recorded levels since population surveys began in 1955 (Can. Wildl. Serv. and U.S. Fish and Wildl. Serv. 1986, Johnson and Shaffer 1987, Reynolds et al. 1990). This prompted the Canadian Wildlife Service (CWS) and U.S. Fish and Wildlife Service (USFWS) in 1982 to initiate investigations of factors thought to influence duck populations in the Prairie Pothole Region (PPR) of Canada (Brace et al. 1987). As part of that investigation, we evaluated mallard nest success and recruitment (Greenwood et al. 1987). The present report focuses on the mallard, gadwall (*A. strepera*), blue-winged teal, northern shoveler (*A. clypeata*), and northern pintail (hereafter called the 5 common species), but also includes data on some other ducks.

The PPR of North America is the primary breeding ground for many ducks; about 80% of the Region is in Canada (Batt et al. 1989). Between 1955–85, an average of 21.6 million ducks used the PPR, representing about 51.1% of the total estimated surveyed population in the Continent. During those years, >50% of the mean total estimated breeding population of 8 of 12 species of ducks that breed in the PPR occurred there, including all 5 common species (Batt et al. 1989). Upland and wetland habitats important to nesting ducks changed considerably in the PPR of Canada after European settlers arrived (Bird 1961, Merriam 1978, Archibold and Wilson 1980). Lynch et al. (1963) estimated that 72% of land in the PPR of Canada produced cereal grains by the mid-1950's. Nearly all the other upland is grazed by livestock.

Studies of nesting ducks conducted in the United States portion of the PPR before this study indicated that duck production was reduced because of low nest success. Cowardin et al. (1985) reported that mallard nest success averaged only 8% in central North Dakota during 1977–80, and concluded that this rate was insufficient to maintain the local breeding population without immigration. Klett et al. (1988) also concluded that nest success was too low for population stability of mallards, gadwalls, blue-winged teals, northern shovelers, and northern pintails in North Dakota, South Dakota, and Minnesota.

Numerous studies of nesting ducks have been conducted in the PPR of Canada (e.g., Milonski 1958, Keith 1961, Smith 1971, Stoudt 1971, Dwernychuk and Boag 1972, Dzubin and Gollop 1972, Fritzell 1975, Oetting and Dixon 1975, Calverley and Boag 1977, Hines and Mitchell 1983). Few, however, provided unbiased estimates of nest success (Johnson 1979) and none attempted to estimate nest success in all habitats at widely separated locations throughout the Region.

Our objectives were to estimate nest success of ducks, especially mallards, at widely separated locations in the PPR of Canada during 1982–85 and to describe primary causes of nest failure. In addition, we examined the relative importance of various components of the nesting process that are associated with mallard production.

Acknowledgments.—We gratefully acknowledge the many agencies and individuals whose assistance made our study possible. For assistance with logistics, field support, data processing and analysis, and report preparation, we thank the administrative and field personnel of Northern Prairie Wildlife Research Center (NPWRC), particularly former Director R. C. Stendell for administrative support; H. F. Duebbert, W. L. Green, A. T. Klett, and J. T. Lokemoen for field work; W. R. Mulvaney, C. L. Nustad, and D. J. Rova for data processing; T. A. Devries, R. C. Khan-Malek, W. E. Newton, and D. J. Twedt for data analysis; T. G. Hanson and K. M. Lahlum for manuscript preparation; D. J. Rova and R. D. Thielman for drafting; B. W. Euliss, H. T. Sklebar, and L. L. Strong for processing satellite imagery; and D. Van Asperen and J. A. Romelfanger for securing and maintaining vehicles. In addition, we extend special thanks to J. M. Callow, D. P. Fellows, D. E. Sharp, M. A. Sovada, and R. O. Woodward of NPWRC who assisted greatly with field work and tabulation of data. R. S. Pospahala, USFWS, Office of Migratory Bird Management, Laurel, Maryland, assisted with study coordination. H. R. Pywell and C. G. Storrs, USFWS, National Wetland Inventory, St. Petersburg, Florida, provided habitat determinations from photographs and prepared maps.

For providing logistic support, assistance with data collection, and loan and storage of field equipment, we thank administrators, field personnel, and conservation officers of the Alberta Department of Forestry, Lands, and Wildlife, especially W. W. MacDonald and H. R. Weaver; Manitoba Department of Natural Resources, especially M. M. Gillespie; and Saskatchewan Department of Parks and Renewable Resources.

For administrative services, loan of field equipment, providing aerial photographs, and assistance with data collection, we thank the staff of the CWS, especially R. K. Brace, F. D. Caswell, G. S. Hochbaum, D. J. Nieman, S. P. Pryor, J. R. Smith, and B. C. Turner. We thank personnel of the CWS Prairie and Northern Wildlife Centre (formerly Prairie Migratory Bird Research Centre), Saskatoon, Saskatchewan, for their support, in particular G. W. Beyersbergen, J. B. Millar, and L. G. Sugden.

For providing assistance with hiring of field technicians, we thank personnel of USFWS Cooperative Fish and Wildlife Research Units, especially E. E. Klaas, Iowa State University; T. S. Baskett, University of Missouri; I. J. Ball, University of Montana; D. H. Rusch, University of Wisconsin; and S. H. Anderson, University of Wyoming. E. K. Fritzell, University of Missouri, also assisted with hiring.

We thank J. E. Austin, R. J. Blohm, R. K. Brace, A. W. Diamond, D. C. Duncan, G. L. Krapu, K. J. Lungle, W. E. Newton, S. P. Pryor, J. S. Ramsey, M. A. Sovada, B. C. Turner, and J. Y. Takekawa for helpful comments on this manuscript.

We especially thank the numerous dedicated field personnel who assisted with data collection and are recognized individually in Sargeant et. al. (1993). Lastly, we are indebted to the many landowners who allowed us to work on their land and offered hospitality and security of their farmyards for equipment storage.

PRAIRIE POTHOLE REGION OF CANADA

The PPR of Canada (Fig. 1) is composed of about 480,000 km^2 in southeastern Alberta, southern Saskatchewan, and southwestern Manitoba (Bellrose 1980). This area is flat to gently rolling and dissected by several rivers. Glacially formed wetlands abound (Gollop 1965), especially in the Missouri Coteau that extends from central Alberta into southeastern Saskatchewan (Kendrew and Currie 1955).

The climate is continental. Snowmelt in spring proceeds from southwest to northeast. Summer temperatures are similar throughout the Region; the July mean is about 18 C. Annual precipitation averages 35.0–45.0 cm (25–30% contributed by snow). June and July have greatest average precipitation. Least precipitation and greatest evaporation occur in southwestern Saskatchewan (Kendrew and Currie 1955, Richards and Fung 1969).

The PPR encompasses 2 physiographic zones: aspen parkland (hereafter called parkland) and prairie (Fig. 1). Parkland is transitional between boreal forest and prairie and contains much deciduous forest (Bird 1961). In the transition to prairie, parkland changes from large wooded areas to an increasingly scattered mosaic of small wooded areas, especially encircling wetlands. Precipitation, ungulates, and fire historically have had important influences on composition of vegetation of the PPR (Bird 1961, Kiel et al. 1972, Daubenmire 1978:190). Presently, weather and farming have greatest impacts (Bird 1961, Merriam 1978, Archibold and Wilson 1980, Turner et al. 1987). Spring-seeded wheat, barley, and canola are the most common grain crops (Sask. Agric. 1982). Cultivated forage crops include mostly alfalfa, sweet clover, and brome grass.

Native perennial vegetation is characterized by robust grasses and forbs in parkland; in prairie, grasses tend to be shorter and forbs less conspicuous (Daubenmire 1978:187). Deciduous trees in parkland are mostly balsam poplar (*Populus balsamifera*) and quaking aspen (*P. tremuloides*). In both parkland and prairie, shrubs include plum and cherry (*Prunus* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), silverberry (*Elaeagnus commutata*), rose (*Rosa* spp.), snowberry (*Symphoricarpos* spp.), and willow (*Salix* spp.). Vegetation of wetlands is similar throughout the PPR (Millar 1969). Emergent wetland plants that provide nesting cover for ducks are grasses, especially reedgrass (*Calamagrostis* spp.) and whitetop rivergrass (*Scolochloa festucacea*), sedges (*Carex* spp.), rushes (*Juncus* spp.), cattails (*Typha* spp.), and bulrushes (*Scirpus* spp.).

STUDY AREA

Definition

We collected data on 17 areas during 1982–85, 9 in parkland and 8 in prairie (Table 1; Fig. 1; *see* Millar [1982, 1983, 1984] and Sargeant et al. [1993] for additional description of areas). A study area was 1.6 km wide by 16.0 km long with a road or trail extending lengthwise through it; each study area consisted of 40 legal quarter-sections (64.8 ha each) (Fig. 1 inset). A study area was superimposed on the air-to-ground comparison segment (hereafter called air–ground segment) of a 0.4-km-wide transect surveyed annually from aircraft by CWS and USFWS during the

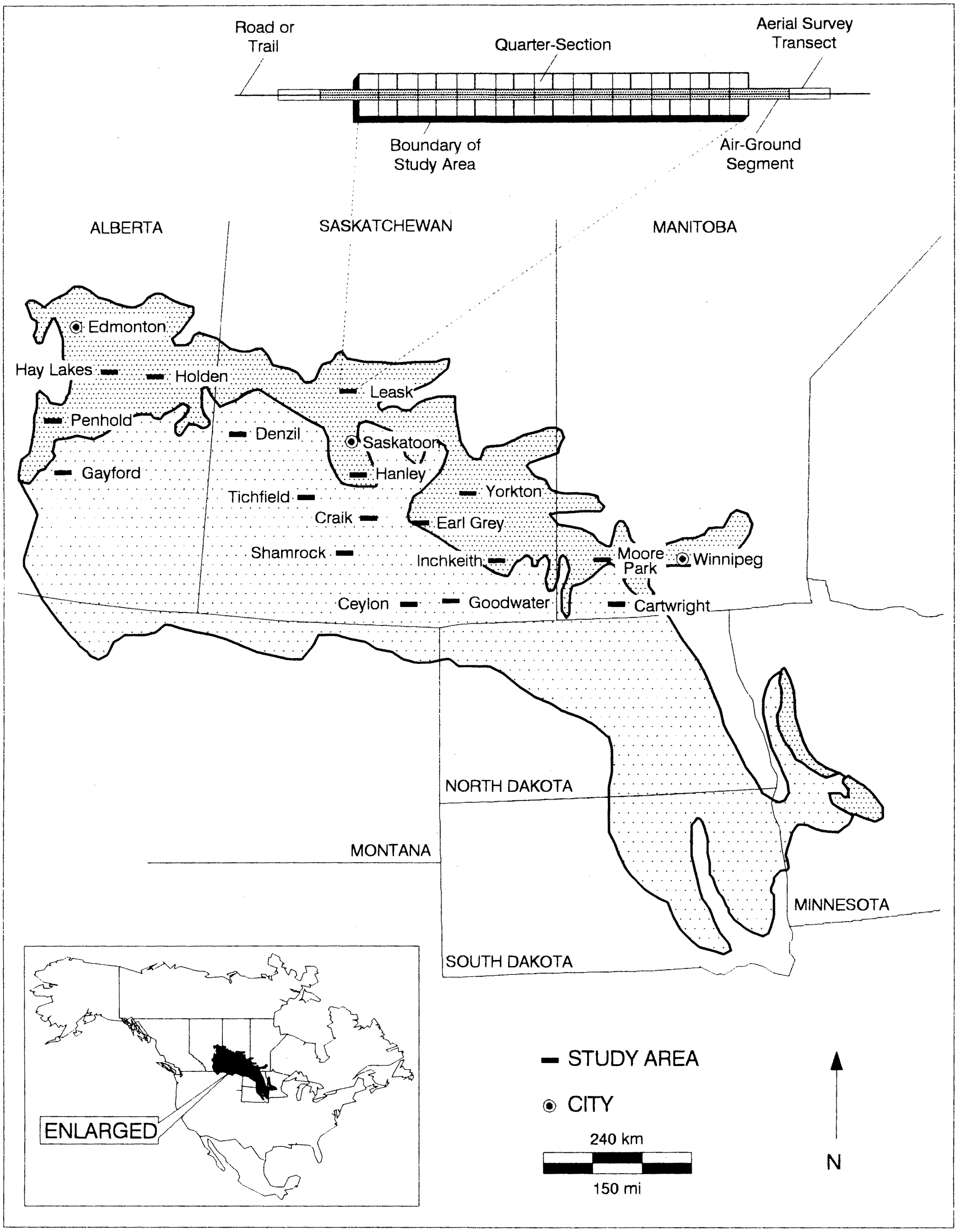

Fig. 1. Prairie Pothole Region of North American showing 1982–85 study areas in parkland (dark shading) and prairie (light shading) physiographic zones. Inset at top shows the Waterfowl Breeding Ground Survey (Off. Migr. Bird Manage., USFWS, Laurel, Md.) aerial transect, the air–ground segment, and the 40 quarter-section study area where we searched for duck nests.

Table 1. Names and locations[a] of areas studied in the Prairie Pothole Region of Canada and years of study.

Study area name	Location				Year
	Section	Township[b]	Range[c]	Meridian	
Parkland					
Earl Grey, Sask.	4	23N	20W	Second	1985
Hanley, Sask.	16	31N	3W	Third	1982–85
Hay Lakes, Alta.	4	49N	21W	Fourth	1983–84
Holden, Alta.	6	49N	14W	Fourth	1983
Inchkeith, Sask.	18	13N	5W	Second	1984–85
Leask, Sask.	4	47N	5W	Third	1984–85
Moore Park, Manit.	9	13N	19W	Principal	1983–84
Penhold, Alta.	4	37N	2W	Fifth	1984–85
Yorkton, Sask.	14	26N	9W	Second	1985
Prairie					
Cartwright, Manit.	21	1N	17W	Principal	1983
Ceylon, Sask.	27	5N	21W	Second	1983–84
Craik, Sask.	15	24N	2W	Third	1984–85
Denzil, Sask.	2	38N	25W	Third	1984–85
Gayford, Alta.	5	27N	26W	Fourth	1985
Goodwater, Sask.	30	5N	14W	Second	1983
Shamrock, Sask.	4	15N	6W	Third	1982–85
Tichfield, Sask.	30	26N	10W	Third	1982

[a] Center of west end of a study area is located at the southwest corner of the designated section, except on Moore Park and Cartwright study areas where the center of west end is at the southwest corner of the southeast quarter of the designated section.
[b] All townships locations are north (N) of the base line at 49° north latitude.
[c] Range locations are west (W) of the designated meridian. All meridians are west of the Principal Meridian at 97°27′43″ west longitude.

Waterfowl Breeding Ground Survey (Martin et al. 1979). Counts of ducks made from the ground on air–ground segments are used to adjust counts made from aircraft. We refer to 1 area studied for 1 year as an "area–year." We divided each study area into 1.6-km-wide by 8.0-km-long halves so we could estimate and examine variability of some parameters within, as well as among, study areas. We refer to one-half of an area studied for 1 year as a "half-area–year."

Selection Criteria

We selected study areas on a nonrandom basis from surveyed transects that had ≥8 pairs/km² of breeding mallards on the air–ground segment during 1977–81 (Off. of Migr. Bird Manage., USFWS, Laurel, Md., unpubl. data). We used surveyed transects as our sampling universe because they have wide geographic distribution and our study supported other research associated with them (Brace et al. 1987); recent aerial photography was available for air–ground segments of these transects, as were annual counts of ducks and wetlands. We selected transects that had relatively high densities of breeding mallards to increase our chances of finding adequate numbers of nests to estimate mallard nest success. We apportioned numbers of study areas similarly in parkland and prairie. We recognize the limitations on inferences that can be made due to our nonrandom sampling, but selection of high density areas was necessary to obtain adequate sample sizes of nests.

In 1982, to evaluate logistics, study procedures, and the amount of nest searching that field personnel could accomplish, we selected 1 area in parkland and 2 in prairie of central Saskatchewan; CWS biologists provided input regarding 1982 selections. We found that a crew of 5 persons could work on 2 areas ≤250 km apart. Resources limited us to 4 such crews in 1983 and 5 each in 1984–85; each crew annually collected data on 2 areas.

We continued data collection for 3 more years beyond 1982 on 2 of the areas. To acquire information on both geographic and temporal variation in nest success with limited resources, we added new areas each year (1983–85) on which we obtained data for 1 or 2 years. We thus obtained data from 7 areas for 1 year, 8 areas for 2 years, and 2 areas for 4 years—a total of 31 area-years (Table 1). The use of the same study area in successive years resulted in some loss of statistical independence, because habitat conditions and predator populations were likely similar in both years.

We selected study areas with the intent of obtaining wide geographic distribution within the PPR of Canada, excluding the southern PPR of Alberta where we did not work because drought there since 1979 had severely reduced numbers of wet wetlands and breeding ducks to the extent that we doubted we could find numbers of nests needed. In 1983, crews worked in the northwestern PPR of Alberta, southern and central PPR of Saskatchewan, and southwestern Manitoba. In 1984, we continued work in those localities and added another crew in the north-central PPR of Saskatchewan.

The decision to work on an area for 1 or 2 years was made annually for logistical convenience. New study areas were selected to obtain maximum distance (≤250 km) from study areas that were retained. We had no personal knowledge of any area before it was selected in 1983–85, except its location and density of mallard breeding pairs. Study areas were retained for a second year without regard to current mallard breeding population, upland or wetland habitat conditions, or number of nests found previously.

Habitat

Habitat composition of study areas was determined by the National Wetland Inventory, USFWS, St. Petersburg, Florida, from color infrared aerial photographs (scale 1:24,000) obtained in May and July 1982. Habitat polygons were defined and data were digitized by means of the Wetland Analytical Mapping System software (Pywell and Niedzwiadek 1980) and converted to Map Overlay Statistical System files (Autometrics, Inc., Fort Collins, Colo., unpubl. rep.). The digitized data were used to create a color-coded habitat map and a text file containing the area and perimeter of each habitat polygon for each study area.

Classification.—We categorized all habitats into the classes of Cowardin et al. (1988): Cropland, Wetland, Hayland, Woodland, Right-of-way, Odd area, and Barren. We replaced their class Grassland with 2 other classes, Grass and Brush, because brush is especially important to mallards for nesting (Cowardin et al. 1985). We defined Grass as untilled land ≥2 ha dominated (>50% areal cover) by grasses and forbs. Brush was untilled land ≥0.2 ha dominated (>50% areal cover) by woody vegetation ≤1 m tall in Grass ≥2 ha (usually native prairie). Wetland included all basins regardless of whether they were wet or dry. Odd area included areas of grasses and forbs <2 ha and an array of other features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland). Barren was composed of areas not suitable for nesting (e.g., road surfaces); we considered areas classified as Barren to be unavailable for nesting. Mean percentages of all habitats in parkland and prairie were weighted by size of study areas.

We used the habitat data base acquired in 1982 for all years, but adjusted it each year as follows for Cropland and Wetland, because those habitats may undergo substantial annual changes that influence their potential use by ducks for nesting. In the first week of May, we apportioned Cropland into standing stubble, tilled stubble, and fallow land (included spring-planted land that was indistinguishable from fallow at that time). Personnel on the ground visually estimated portions of every quarter-section in each category. Of the 3 types of Cropland, we considered only standing stubble to be suitable as nesting cover; amounts of tilled stubble and fallow land (considered not suitable for nesting) were added to Barren that year to create a class

Table 2. Size (ha) of study areas in the Prairie Pothole Region of Canada and composition (%) of landscapes based on interpretation of aerial photography obtained in May and July 1982. Means were weighted by size of study area. Rows sum to 100% with rounding errors.

Study area	Size (ha)	Habitat (%) Cropland	Grass	Brush	Wetland	Hayland	Woodland	Right-of-way	Odd area[a]	Barren[b]
Parkland										
Earl Grey	2,638	80	1	<1	8	<1	0	2	8	1
Hanley	2,691	70	8	3	11	0	0	2	6	1
Hay Lakes	2,700	44	12	<1	16	12	5	3	8	1
Holden	2,658	45	24	<1	17	0	<1	3	9	1
Inchkeith	2,683	71	10	<1	5	0	<1	4	8	1
Leask	2,691	40	23	<1	12	3	12	3	7	1
Moore Park	2,729	62	7	<1	14	1	2	3	11	1
Penhold	2,677	50	19	0	19	2	3	2	5	1
Yorkton	2,708	45	22	<1	11	2	9	2	8	<1
$\bar{x}$	2,686	56	16	1	13	2	4	3	8	1
Prairie										
Cartwright	2,719	66	16	0	7	3	0	3	5	1
Ceylon	2,666	56	28	3	9	0	0	1	1	1
Craik	2,646	84	2	<1	7	0	0	2	3	1
Denzil	2,691	76	9	<1	7	0	0	3	4	1
Gayford	2,699	30	37	4	14	8	0	2	3	1
Goodwater	2,661	50	27	2	9	7	0	3	2	1
Shamrock	2,693	59	22	2	7	5	0	2	2	1
Tichfield	2,662	75	9	2	7	<1	<1	2	3	1
$\bar{x}$	2,680	62	22	2	8	3	<1	2	3	1
Overall $\bar{x}$	2,683	59	19	1	11	3	2	2	5	1

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).
[b] Barren included all areas not suitable for nesting (e.g., road surface).

called Unsuitable. Although availability of standing stubble changed during the nesting season because of tillage, we did not change the percentage of Cropland we considered to be suitable as nesting habitat after our May assessment. We calculated the mean percentage of Cropland that was standing stubble annually; means were weighted by area of Cropland available on individual study areas in 1982. We did not adjust Cropland values to reflect increasing presence of growing grain that began to emerge in early to mid-June.

We considered vegetation in temporary and seasonal wetlands to be available for nesting if basins were dry at the time of the annual Waterfowl Breeding Ground Survey in May (*see* Weather and Wetland Conditions). If temporary and seasonal wetlands were wet in May, we considered them unsuitable for nesting and added the area of those wetlands that year to Unsuitable. We considered emergent vegetation in semipermanent wetlands to be available for nesting in the current year regardless of whether the basin was wet or dry, but considered only 75% of this habitat to be suitable for nesting. Aerial photographs and ground surveillance showed that about 25% of the emergent vegetation in semipermanent wetlands usually was not suitable for nesting (e.g., too sparse); therefore, we reduced the area of emergent semipermanent wetland habitat by 25% each year and added that amount to Unsuitable. Areas of open water also were added to Unsuitable.

Composition.—Cropland averaged 59% of the landscape on study areas (56% in parkland and 62% in prairie) (Table 2). However, in early May an average of only 16% of the landscape was standing stubble in all area–years (13% in parkland and 20% in prairie). Remaining Cropland had been tilled or was fallow the previous year (Table 3). Standing stubble that we considered suitable as nesting habitat averaged 16% of the landscape in all area–years.

Grass averaged 19% of the landscape on study areas (Table 2). Largest contiguous areas of Grass on study areas were 4–8-km^2 pastures managed by the Prairie Farm Rehabilitation Administration, municipal agencies, or private landowners on the Ceylon, Gayford, Goodwater, Holden, Leask, Penhold, Shamrock, and Yorkton study areas. Brush was a minor habitat component in areas of native prairie Grass and averaged 1% of the landscape on study areas (Table 2).

Wetland averaged 11% of the landscape on study areas (Table 2), but an average of only 4% of the landscape was Wetland that we considered suitable as nesting cover in all area–years. Estimated density of wetlands ranged from 10/km^2 on the Leask Study Area to 50/km^2 on the Moore Park Study Area (Table 4).

Odd area averaged 5% of the landscape on study areas (Table 2) and tended to be least available on study areas in the prairie where there were few trees to interfere with tillage. In the parkland, Odd area often was composed of narrow bands of shrubs and trees that encircled wetlands in cultivated fields.

Woodland averaged 4% of the landscape in parkland, but was nearly absent (<1%) from most study areas in prairie (Table 2). Contiguous areas of Woodland were seldom >65 ha and most were grazed.

Hayland averaged 3% and Right-of-way averaged 2% of the landscape on study areas (Table 2). Right-of-way was mostly along roads. In most years, forage crops in Hayland and vegetation in Right-of-way were mowed in late June.

Barren averaged 1% of the landscape on all study areas (Table 2). The total area classified as Unsuitable (Barren plus portions of Cropland and Wetland that were not suitable for nesting) averaged 50% of the landscape in all area–years.

Wetlands and Weather

We estimated densities of wetland basins by class (Cowardin et al. 1988) on individual study areas and percentages that were wet in May annually, 1982–85, from unpublished data obtained during the Waterfowl Breeding Ground Survey (Off. Migr. Bird Manage., USFWS, Laurel, Md.). Because these data were for the 0.4-km-wide air–ground segments, we first converted numbers of basins by wetland class to density (basins per km^2) and then extrapolated to estimate density of each class on each 1.6-km-wide study area. We determined from annual Waterfowl Breeding Ground Survey results the percentage of basins that were wet. Annual mean percentages of wet basins by class per square kilometer were weighted by number of basins by class per square kilometer to estimate the annual mean percentage of wet basins by class per area–year.

Annual precipitation and temperature statistics were obtained from recording stations nearest to our study areas (Table 5) (Atmos. Environ. Serv., Cent. Reg., En-

Table 3. Amount of Cropland available (ha) and amount considered suitable (%) as nesting cover (uncultivated standing stubble) in the first week of May on study areas in the Prairie Pothole Region of Canada. Means were weighted by available Cropland.

Study area	Cropland available (ha)	Suitable for nesting (%)			
		1982	1983	1984	1985
Parkland					
Earl Grey	2,102				41
Hanley	1,889	17	26	12	69
Hay Lakes	1,178		19	19	
Holden	1,208		60		
Inchkeith	1,917			29	26
Leask	1,068			9	17
Moore Park	1,700		16	7	
Penhold	1,342			5	13
Yorkton	1,214				7
$\bar{x}$	1,513	17	27	13	33
Prairie					
Cartwright	1,786		13		
Ceylon	1,506		40	18	
Craik	2,223			24	50
Denzil	2,058			17	55
Gayford	808				61
Goodwater	1,319		36		
Shamrock	1,585	45	32	29	44
Tichfield	2,009	72			
$\bar{x}$	1,662	35	29	22	51
Overall $\bar{x}$	1,583	29	28	17	40

Table 4. Estimated number of temporary (T), seasonal (S), and semipermanent (SP) wetlands (Cowardin et al. 1988) per km² on study areas in the Prairie Pothole Region of Canada and percentage that were wet in May[a]. Means were weighted by estimated number of wetlands/km².

				Wet wetlands (%)											
	Estimated no./km²			1982			1983			1984			1985		
Study area	T	S	SP	T	S	SP	T	S	SP	T	S	SP	T	S	SP
Parkland															
Earl Grey	19	14	6										74	97	100
Hanley	2	28	11	33	62	75	58	71	89	0	6	38	75	91	97
Hay Lakes	9	8	12				40	61	89	18	35	78			
Holden	4	8	5				35	46	97						
Inchkeith	18	4	2							6	43	91	67	93	100
Leask	6	1	3							19	67	100	59	67	100
Moore Park	11	24	15				62	94	100	11	43	90			
Penhold	1	10	5							17	21	73	33	39	57
Yorkton	7	13	14										44	86	96
$\bar{x}$	9	12	8	33	62	75	50	75	94	11	26	74	65	84	93
Prairie															
Cartwright	1	13	3				33	70	94						
Ceylon	8	6	4				55	88	96	4	24	64			
Craik	11	10	3							1	14	83	80	86	100
Denzil	10	5	2							41	66	87	75	97	92
Gayford	6	4	6										14	37	83
Goodwater	4	11	7				24	83	100						
Shamrock	4	9	7	28	80	98	35	84	98	0	2	44	3	20	76
Tichfield	12	9	4	53	92	100									
$\bar{x}$	7	8	5	47	86	99	42	80	98	14	21	62	58	60	84
Overall $\bar{x}$	8	10	6	45	71	87	47	77	95	12	24	71	62	77	90

[a] Wet implies visible standing water. Data provided by Off. Migr. Bird Manage., U.S. Fish and Wildl. Serv., Laurel, Md., based on assessment conducted in May during annual Waterfowl Breeding Ground Survey (Martin et al. 1979).

viron. Canada, Winnipeg, Manit. or Atmos. Environ. Serv., West. Reg., Environ. Canada, Edmonton, Alta., unpubl. data). Field crews reported local weather conditions on individual study areas, especially storms with potential to adversely affect nesting.

Annual Conditions.—In early May 1982, an average of 45% of temporary, 71% of seasonal, and 87% of semipermanent wetlands overall were wet (Table 4). A storm during 26–29 May produced heavy snowfall on Hanley and especially on Tichfield (6.9 cm water content) study areas and 7.5 cm of rain on Shamrock Study Area; subfreezing temperatures persisted for 2–3 days afterward. Total precipitation was above average on those study areas during the 1982 nesting season (Table 5).

Wetland conditions in early May 1983 were similar to 1982. Two storms during 8–14 May produced rain and snow on Shamrock, Hanley, Goodwater, Ceylon, Moore Park, and Cartwright study areas. However, total precipitation during the nesting season was below average on 5 of those areas (Table 5). Higher than average precipitation on Hay Lakes and Holden study areas that year resulted from 20.0 cm of rain during 18–30 June; low-lying areas flooded and depth of water in many wetlands increased up to 90.0 cm on those study areas.

Drought impacted 6 of 10 areas studied in 1984. An average of 12% of temporary, 24% of seasonal, and 71% of semipermanent wetlands overall were wet in May (Table 4). Precipitation during the nesting season was 13–52% below average on areas studied that year (Table 5). Only Denzil and Leask study areas had precipitation well above average (22 and 66%).

Ample wet wetlands were available in May 1985 on Craik, Earl Grey, Hanley, Inchkeith, and Leask study areas (Table 4). Precipitation during the nesting season

Table 5. Departure (%) from 30-year April–June average precipitation amounts (cm) at individual study areas in the Prairie Pothole Region of Canada.

Study area	Reporting station	30-year average (cm)	Departure (%)			
			1982	1983	1984	1985
Parkland						
Earl Grey	Strasbourg[a]	4.7				+17
Hanley	Dundurn[a,b]	4.1	+17	+7	−32	+23
Hay Lakes	Camrose[c]	4.8		+54	+2	
Holden	Camrose[c]	4.8		+54		
Inchkeith	Kipling[a]	5.3			−30	−19
Leask	Prince Albert[a]	4.4			+66	+36
Moore Park	Brandon[a]	5.3		−36	+4	
Penhold	Red Deer[c]	5.3			−13	−46
Yorkton	Yorkton[a]	4.6				+5
Prairie						
Cartwright	Pilot Mound[a]	6.2		−35		
Ceylon	Ceylon[a]	5.6		−27	−52	
Craik	Tugaske[a]	4.7			−28	−11
Denzil	Scott[a]	4.1			+22	+8
Gayford	Calgary[c]	5.7				−49
Goodwater	Midale[a]	5.3		−32		
Shamrock	Shamrock[a]	4.3	+28	−51	−16	−42
Tichfield	Beechy[a]	4.0	+28			

[a] Average and monthly amounts obtained from Atmos. Environ. Serv., East. Reg., Environ. Canada, Winnipeg, Manit.
[b] Dundurn station closed in 1985; average and monthly amount in 1985 are for Colonsay.
[c] Average and monthly amounts obtained from Atmos. Environ. Serv., West. Reg., Environ. Canada, Edmonton, Alta.

on the 10 areas studied in 1985 was below average on 5 and near or above average on the remaining (Table 5).

Breeding Duck Populations

Ground counts of breeding ducks were made annually by CWS and USFWS personnel in mid-May on each air–ground segment (Martin et al. 1979). Ducks were tallied by species and social grouping for each wet wetland; ducks in upland were assigned to the nearest wetland. Social groups for each species were lone males, lone females, flocked males (2–4 individuals), pairs, and grouped birds (≥5 individuals). Numbers of lone males, flocked males, and pairs were summed to estimate total indicated pairs for each species. Because our study areas did not include entire air–ground segments, we extracted the densities of indicated pairs of the 5 common species from annual ground counts obtained for portions of air–ground segments that were included in our study areas. Densities of the 5 common species on the 0.4-km-wide air–ground segments were extrapolated on the basis of area to arrive at the number of breeding pairs on each half-area–year. Estimated numbers of pairs in each half-area–year were summed to obtain total breeding pairs for each area–year (Tables 1–5 of Appendix A).

Predator Community

Sargeant et al. (1993) reported the makeup of predator communities on our study areas during 1983–85. Species present that are known to prey on nesting ducks or their eggs included the coyote (*Canis latrans*), red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), badger (*Taxidea taxus*), mink (*Mustela vison*), weasel (*Mustela erminea* and *M. frenata*), Franklin's ground squirrel (*Spermophilus franklinii*), American crow (*Corvus brachyrhynchos*), black-billed magpie (*Pica pica*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), red-tailed hawk (*B. jamaicensis*), ferruginous hawk (*B. regalis*), and great horned owl (*Bubo virginianus*).

Composition of predator communities

and abundance of individual species varied considerably among study areas, but varied little annually (Sargeant et al. 1993). Sargeant et al. (1993) found at least 5 species of predatory mammals and 6 species of predatory birds on every study area. The striped skunk and great horned owl were present on all study areas. Other predators were more specific to certain physiographic zones. Franklin's ground squirrel and red-tailed hawk were more common on study areas in parkland; badger, Swainson's hawk, and ferruginous hawk were more common on study areas in prairie.

Coyotes, red foxes, or both, were present on many study areas, but the 2 species were seldom present on the same parts of individual study areas (Sargeant et al. 1993). Coyotes often were associated with more remote parts of study areas away from human habitation, such as large pastures; red foxes were found mostly in cultivated land.

METHODS

Data Collection

Nest Searches.—We searched vegetation to find duck nests in all habitats considered suitable for nesting; habitats classified as Unsuitable were not searched. A nest was defined as ≥ 1 egg tended by a female when found (Klett et al. 1986). Habitat on each study area was systematically searched 3 times annually. Search periods began the first week of May, fourth week of May, and second week of June. During each period, a crew usually completed searching 1 study area (7–8 days required) before the second area was started. Daily searches were conducted between 0600 and 1400 hours. On each study area, individual fields were searched in the same order during each search period. Searches in Cropland stubble fields were not repeated after the field was tilled.

Where possible, 2-person teams searched vegetation in upland habitats with chain drags (8–9-mm-diam. by ≤ 80-m-long) towed by vehicles, using procedures similar to those described by Higgins et al. (1969). Where chain drags could not be used effectively, persons walked and pulled rope drags or used switches to beat the vegetation and flush nesting females. We searched most habitat suitable for nesting on prairie study areas where there were few trees. In parkland, trees and shrubs prevented use of chain drags in many places. There, to distribute the search effort throughout the study area, we searched completely all nesting habitat in individual quarter-sections or portions of quarter-sections scattered along both sides of the center road. We augmented scanty samples of nests in habitats (mostly Wetland, Right-of-way, and Odd area) on some study areas (n = 20 area–years) by searching a few sites ($\bar{x}$ = 8/area–year) of the same class within 0.8 km of the study area.

We marked each nest with an individually-numbered willow stick (1–1.5 m) flagged with a small piece of pink plastic tape, or noted the nest location in relation to a natural feature (e.g., prominent rock or fence post). Marker sticks were placed upright 4 m from the nest. Nest locations were plotted on aerial photographs. Nests were revisited about every 7–10 days until ≥ 1 egg hatched or the nest was abandoned or totally destroyed. Data recorded upon finding each nest were duck species, date, location, habitat class, type of vegetation within 1 m, number of eggs, and incubation stage (Weller 1956, Klett et al. 1986).

On each revisit to a nest, we verified species identity and recorded date, number of eggs, and completed clutch size (if known). On the last visit we recorded fate and, if the nest failed to hatch, suspected cause of failure. A nest was deemed successful if ≥ 1 egg hatched, as determined by presence of shell membranes (Klett et al. 1986) or ducklings in the nest bowl, and unsuccessful if all eggs were destroyed or missing. If ≥ 1 whole egg remained and the nest was no longer tended (eggs cold and additional eggs not being deposited daily), we classified the nest as abandoned; such nests also were deemed unsuccessful. For nests that appeared to have been abandoned on the day of discovery, we attributed abandonment to investigator influence. For nests that were abandoned after some eggs were destroyed, we attributed abandonment to predator influence. Nest fate was classified as unknown if the nest could not be relocated.

We assigned cause of all nest failures to predation, agricultural equipment, weather, or other (e.g., flooding, fire, trampling); nests that failed because of abandonment (except investigator-influenced) were included in the appropriate category of failure. Cause of nest failure was called unknown if we suspected >1 agent was involved, or if the cause was ambiguous (e.g., nest that appeared to have been destroyed by tillage might have been destroyed by a predator before tillage).

Adult Mortality.—During 1983–85, field personnel recorded species, sex, and location of all fresh (i.e., current year) duck remains found on study areas and (if necessary for identification) collected remains. Most remains were found opportunistically. In addition, all coyote and red fox dens and raptor nests were examined when found for presence of remains; dens were not excavated and <10% of raptor nest bowls were examined. When remains were not collected, they were hidden or marked to avoid counting them again. Collected remains were examined later to determine the number of individual ducks represented and to identify each as to sex and lowest taxon possible. We assumed all ducks found on a study area were from breeding populations on that area.

Data Analysis

Nest success for an area with >1 habitat class is a function of the number and success of nests in each habitat in that area. For many study areas, our samples of nests probably did not reflect their true distribution among habitat classes; we were denied access to some land, and we could not search all habitats in equal proportion (e.g., Woodland and Wetland were more difficult to search than was Grass; thus we searched smaller proportions of these habitats than of Grass). We attempted to minimize the effects of unequal search effort on our estimates of nest distribution for each of the 5 common species in all habitat classes on each study area by deriving an index to the number of nests initiated in each habitat class on each half-area–year; this exercise, however, did not overcome other potential biases with nest drags (e.g., unequal effectiveness in different habitats). The index was the product of the total amount of habitat in each class in the half-area–year, the number of breeding pairs in the half-area–year, and species preference for nesting in the particular habitat class. By scaling the index values to sum to one, we obtained estimates of the proportions of nest initiations in each habitat class.

We measured the amount of habitat available in each class (Table 2) and number of breeding pairs (Tables 1–5 of Appendix A), but had to derive preference values (*see* below). Preference of a species for a habitat was defined by Klett et al. (1988) as the estimated probability that a female will select a particular habitat class for nesting, given that all habitat classes are equally available.

Habitat Preference.—We used all nests of all of the 5 common species regardless of their fates to derive habitat preference values. For each species, we pooled all nests found in all habitat searched in each habitat class in all area–years. In combining data in this manner to derive preference values, we accepted the following assumptions as being reasonable: (1) that preference for nesting in a habitat by a species is an innate behavioral preference and was similar in all area–years and (2) that our procedures to find nests were about as effective in all habitats and all stages of nesting.

We used a linear model (Appendix B) to estimate nest densities among habitats and study areas; large differences existed in amount of habitat searched and in numbers of nests found in some habitats in some area–years. A key feature of this model, like the model we used to improve our estimates of daily survival rates (DSR's) in the following section, is that habitat effects did not interact with other effects.

We included in the model effects for area–year, half-area–year within area–year, habitat, and number of nest searches. Number of searches was included because not all habitat polygons could be searched 3 times (e.g., stubble fields in Cropland usually could be searched only once before they were tilled). We used a transformed variable, $\log([N + 0.0001] \div A)$ as the dependent variable, where N is the number of nests found for a species and A is the area searched. The log transformation was invoked because we believed the effects of the explanatory variables were more likely to be proportional than additive. We added 0.0001 to avoid difficulties involved with taking the log of zero. We fitted the linear model by the method of weighted least squares (Snedecor and Cochran 1980) with weights equal to the product of number of breeding pairs and area of each habitat class searched in individual half-area–years. Theoretically, these weights reflected the relative precision of each density estimate. Habitat preference values were calculated by scaling least-squares estimates of habitat effects so that they summed to 1.0.

Nest Success.—We estimated DSR's of nests by the Mayfield method as modified by Johnson (1979). We excluded nests that showed evidence of egg depredation or that contained parasitically-laid eggs when found, and all nests that were abandoned due to investigator influence or that contained eggs broken by an investigator. After analyses were performed, (for ease of interpretation) we converted DSR to nest success (P), where $P = (\text{DSR})^I$ and I is the average duration of the laying period plus incubation interval in days. The laying interval was allowed to vary with clutch size if possible. If not possible, we used average laying and incubation intervals from Klett et al. (1986).

The variance of an estimated DSR is inversely proportional to the number of exposure days (Johnson 1979), and (for certain species) differences in numbers of exposure days among some habitat classes, study areas, and years greatly influenced the precision of our DSR estimates. We used a linear model (PROC GLM, SAS Institute, Inc. 1989) fitted by the method of weighted least squares, with weights equal to the number of exposure days (Snedecor and Cochran 1980) to overcome imbalance due to small numbers of exposure days in some categories. The initial model included effects for area–year, half-area–year within area–year, habitat, species, and interactions between area–year and species. We tested for significant ($P < 0.05$ throughout, unless otherwise noted) effects by extending the method of Johnson (1990) to multiple effects. We subsequently removed interactions between area–year and species because they were not significant and fitted a reduced model involving the remaining effects (Appendix C). Analysis indicated all remaining effects were significant ($P < 0.05$) except species ($P = 0.16$). We chose to leave species effects in the model because early-nesting species have lower nest success than late-nesting species (Klett et al. 1988) and we wished to retain this option in our analysis. Our assumption that habitat effects were similar among area–years and species precluded comparisons of nest success by habitat on individual study areas.

Nest Success by Study Area.—We derived independent estimates of DSR's by habitat class for each half-area–year and each of the 5 common species. We weighted the DSR's of nests in each habitat class and half-area–year by the estimated proportion of nests initiated in that habitat class and half-area–year; weighted DSR's were pooled and averaged across all habitat classes to estimate the DSR for the entire area–year. Before weighting and pooling, we tested for differences in DSR's by habitat class between halves of each area–year using linear contrasts (Snedecor and Cochran 1980). We used pooled estimates by habitat class for halves where DSR's did not differ ($P > 0.10$). We detected significant differences in DSR's by habitat class between east and west halves of Yorkton (1985), Ceylon (1983, 1984), Hanley (1982, 1985), Leask (1985), Denzil (1985), and Holden (1983) study areas. The 0.10 level of significance was chosen for this analysis because we believed that nest success by area–year would be affected less by treating the halves as being different, when they were in fact similar, than by treating them as being similar, when they were actually different.

Nesting Chronology.—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 one day for each day of incubation minus 1. We calculated median date of nest initiation and interquartile range of initiation dates for each of the 5 common species in each area–year. For each of the 5 common species, we performed multiple regression analyses relating (1) median date of nest initiation and (2) interquartile range of initiation dates to nest success, percentage of seasonal wetlands that were wet in May, and average temperature and total precipitation each month, April through June. We used the interquartile range (the difference between third and first quartiles) as a measure of the central span of the nesting period. The median date of nest initiation and interquartile range of initiation dates were compared among the 5 common species with analysis of variance. When an overall difference was detected, linear contrasts were used to identify which species were different. Each area–year for which we had ≥10 nests was assigned a weight equal to the square root of the number of nests. Area–years with <10 nests were not used because we considered them inadequate for estimating these nesting parameters.

Nest Fate.—We determined for all of the 5 common species combined in each habitat class of each half-area–year the percentage of unsuccessful nests that failed due to predation, agriculture, and other agents, and the percentage of abandoned nests caused by predation, weather, and other agents; nests abandoned because of investigator activity had been excluded previously. We combined nests of the 5 common species to increase sample size. By doing so, we assumed that all nests in a given habitat were at equal risk to all agents responsible for nest failure. In half-area–years where data on causes of nest failure in a particular habitat class were inadequate, we used an average value for that habitat class calculated from data for all area–years. We determined percentage of nest failures caused by various agents in a half-area–year; rates were weighted by a value equal to the product of habitat preference of each species and availability of habitat in that half-area–year. To obtain an estimate for each area–year, we weighted the rates for each half-area–year by number of pairs of the 5 common species in each half-area and combined them.

Nest Success and Percentage Cropland.—We conducted an analysis of covariance (Milliken 1990) to examine the relation between nest success (the response variable) and percentage of Cropland (includes standing stubble, tilled stubble, and fallow land) and physiographic zone (parkland or prairie). We attempted to predict (within the observed range of nest success and habitat conditions) the threshold level of Cropland availability above which nest success would be insufficient to sustain populations of the 5 common species. Minimum threshold levels of nest success assumed to be necessary for population stability were 15% for mallards (Cowardin et al. 1985), 15% for northern pintails (Klett et al. 1988), and 20% each for gadwalls, blue-winged teals, and northern shovelers (Klett et al. 1988). Mean nest success among area–years was examined to determine if nest success depended on percentage Cropland available in parkland or prairie. Significant results ($P <$ 0.05) were tested separately for each species to isolate which physiographic zone was responsible for rejection of the null hypothesis that regression slopes were equal to zero. After we established the relation between nest success and percentage of Cropland by zone, we predicted percentage of Cropland at suggested thresholds of nest success using the "inverse prediction" procedure described by Neter et al. (1985). Statistical comparisons were performed with GLM procedures of SAS (SAS Institute, Inc. 1989).

Seasonal Variation in Nest Predation Rate.—We examined seasonal effects on nest success by comparing daily rates of nest predation for each of the 5 common species among search periods. This rate is defined as number of nests unsuccessful because of predation, divided by total exposure days. We compared daily predation rates for mallard and northern pintail nests under observation in first, second, or third search periods. For the later-nesting gadwalls, blue-winged teals, and northern shovelers, we compared rates only for second and third periods because insufficient nests were found in the first period. We used only nests found in uplands and dry wetlands and combined all nests in these categories. We excluded nests located over water because our sample size was insufficient for separate analysis.

We used daily rate of nest predation as the response variable in our analysis. Explanatory variables were area–year, search period when nest was found, and the interaction between these 2 variables. To examine interaction with search period, it was necessary to exclude (Appendix D) area–years for individual species unless at least 1 nest was found during each search period. We were left with 21–29 area–years for each of the 5 common species. Observations were weighted by the number of exposure days. Chi-squared statistics for each effect were calculated from Type III sums of squares (Johnson 1990).

Detection of a significant interaction between area–year and search period for 4 of the 5 common species prompted us to examine more closely the relation between drought conditions and daily rate of nest predation. To do this we grouped area–years into 3 wetness intervals by means of a centroid clustering procedure (SAS Institute, Inc. 1989). Intervals were based on percentage of seasonal wetlands in each area–year that were wet in May and on departure in total precipitation from the long-term average for that area during April through June. The 3 intervals were dry (<43% of wetlands wet and precipitation <−4% of average), moderate (>70% of wetlands wet and precipitation <−11% of average), and wet (>46% of wetlands wet and precipitation >7% of average). Within each wetness category (dry, n = 11; moderate, n = 7; wet, n = 13), we used linear contrasts to examine interactions between area–year and search period by species, again with daily rate of nest predation as the response variable.

Adult Mortality.—We compared species composition of ducks found dead with species composition of ducks in the breeding population using a chi-squared goodness-of-fit test. Comparisons were done separately for each year, 1983–85. For the 5 common species, we used an r-sample binomial test (Bain and Engelhardt 1987) to examine the null hypothesis that male and female ducks were killed in proportion to their abundance in the breeding population. We assumed that breeding populations contained equal proportions of males and females, although continental populations of these species are thought to contain more males than females (Bellrose 1980). We first simultaneously tested the null hypothesis for all years for each species to determine overall significance (P = 0.05). Significant results for a species were then examined by individual year to isolate the source of significance. For each species, we excluded years with <10 specimens identified to sex, because distribution of the test statistic is unknown for small samples.

Components of Mallard Production.—We evaluated mallard reproduction during 1983–85 in relation to variation in component parameters and partitioned this variation into geographic and temporal factors. Production of ducks requires that pairs are available to populate the breeding area and that wetlands are available in spring to attract and support the breeding pairs and ducklings produced. Females must nest, some nests must hatch and produce young, and some of those young must survive to fledge.

This process can be represented as follows:

$$\text{Number Fledged} = \text{Wetlands} \times \frac{\text{Pairs}}{\text{Wetland}} \times \frac{\text{Nests}}{\text{Pairs}} \times \frac{\text{Hatched Nests}}{\text{Nest}} \times \frac{\text{Fledged}}{\text{Hatched Nest}}. \quad (1)$$

By determining which variables on the right-hand side of equation (1) most closely correlate with Number Fledged, we can hypothesize which ones are most influential in their production. The method is similar in principle to key-factor analysis (Varley and Gradwell 1960, Podoler and Rogers 1975).

We used data for the mallard for this exercise, because it was of special interest in other research that our study supported (Brace et al. 1987) and was generally the most numerous duck species on all area–years. We lacked information on the survival of ducklings on areas we studied, so the final component could not be determined. This left

$$\text{Hatched nests} = \text{Wetlands} \times \frac{\text{Pairs}}{\text{Wetland}} \times \frac{\text{Nests}}{\text{Pair}} \times \frac{\text{Hatched Nests}}{\text{Nest}}. \quad (2)$$

By estimating, for each half-area–year, the number of Hatched Nests and the 4 components on the right-hand side of equation (2), we determined the relative importance of each of them in relation to the variability of Hatched Nests.

An alternative formulation is

$$\text{Hatched Nests} = \text{Pairs} \times \frac{\text{Nests}}{\text{Pair}} \times \frac{\text{Hatched Nests}}{\text{Nest}}. \quad (3)$$

This has the disadvantage of ignoring the impact of wetland numbers but shows more directly the effect of the number of pairs on production.

Not all of these variables were directly estimated in our field study; some had to be calculated from other variables. The number of Hatched Nests was determined by taking the number of successful mallard nests found on the area searched within each half-area–year and scaling it upwards to account for the amount of nesting habitat on that half-area–year that was not searched.

Pairs and Wetlands were measured directly. For this analysis we used the total number of temporary, seasonal, and semipermanent wetlands that were wet in May.

The Nest-per-Pair value required an estimate of the total number of nests initiated on a half-area–year, as follows:

1. Nest success rate estimates the number of successful nests divided by the total number of nests initiated.
2. Nest success was independently estimated by the Mayfield method (Johnson 1979).
3. The total number of nests initiated thus can be estimated as the number of successful nests divided by the nest success rate (Miller and Johnson 1978).
4. The resulting value is divided by the number of Pairs to yield the Nests-per-Pair value.

The Hatched Nests-per-Nest component is the nest success rate.

Some derived values were clearly out of line because mallard populations on each half-area–year were not closed (i.e., birds could freely move into and out of each area) and, possibly, because of errors in estimating the quantities. For example, on the west half of the Ceylon Study Area in 1984, only 1 successful mallard nest was observed. The estimated hatch rate of mallard nests was only 0.002, so the single successful nest is estimated to represent $1 \div 0.002 = 500$ initiated nests. This is far too many for the 20 mallard pairs estimated to be on that area. Accordingly, we constrained the number of nests per pair to be no greater than 4. This constraint was imposed for only a few ($n = 7$) half-area–years.

We determined the relations between Hatched Nests and each component by examining bivariate plots and calculating correlation coefficients. Because of the multiplicative form of equation (2), logarithms were taken to yield an additive model:

$$\log(\text{Hatched nests}) = \log(\text{Wetlands}) + \log(\text{Pairs/Wetland}) + \log(\text{Nests/Pair}) + \log(\text{Hatched Nests/Nest}). \quad (4)$$

This transformation precluded the use of half-area–years with no hatched nests because the logarithm of zero is undefined. Correspondingly, for a half-area–year with no hatched nests, the analogous model for equation (3) is

$$\log(\text{Hatched Nests}) = \log(\text{Pairs}) + \log(\text{Nests/Pair}) + \log(\text{Hatched Nests/Nest}). \quad (5)$$

Geographic and Temporal Effects on Mallard Production.—We estimated the relative contributions of spatial and temporal factors to variation in selected variables associated with mallard production; variables were number of temporary, seasonal, and semipermanent wetlands that were wet in May, number of breeding pairs, and nest success rate.

We used a random-effects linear model to estimate the relative contributions of temporal and spatial components of variance. The model assumes that the value of the selected variable can be expressed as a linear combination of the above components in addition to a component for inherent variability. This analysis was complicated by not studying all areas in all years; variance components for study area and year are confounded with the interaction component. We recognized early this limitation in study design, but could not avoid it because we wanted to study more areas in total than could be evaluated in any single year. To minimize difficulties presented by the design, we divided study areas into 5 groups. One consisted of areas studied during both 1983 and 1984. A second was made up of areas studied during both 1984 and 1985. The remaining 3 groups included areas studied only in 1982, 1983, and 1985, respectively. This grouping allowed us to analyze balanced designs. A disadvantage is that the 2 areas studied in all years are included twice in the analysis.

We performed a 2-way (by study area and year) analysis of variance on each of the first 2 groups. For the 3 other groups, we did a 1-way (by study area) analysis of variance. The components of variance were estimated by equating mean squares with their expected values and solving for the unknown components (Searle 1971).

Because we performed an analysis on each of the 5 groups, we obtained 2 nearly independent estimates (from the first 2 groups) of each variance component associated with year and 5 of each associated with study area. These estimates were pooled by weighting each mean square by its degrees of freedom and averaging. Expected mean squares were obtained in a similar manner. The variance components were then estimated as before. Coefficients of variation (CV) of each component (Error = CV_E, Study area = CV_{SA}, and Year = CV_Y) were obtained by dividing the square root of the variance component by the mean of that variable.

RESULTS

We found 5,354 duck nests that were usable for estimating chronology of nesting and habitat preferences, but excluded 510 of these for estimating survival rates. Excluded nests had been parasitized by another species when found (143); contained broken eggshells or egg content, suggesting predation had already occurred (56); contained eggs accidently broken by an investigator (108); were abandoned on the day found, most likely because of our influence (129); or could not be relocated (74). Of the remaining 4,844 nests, 33% were mallard, 18% blue-winged teal, 15% northern pintail, 11% northern shoveler, 10% gadwall, 4% American wigeon (*Anas americana*), 4% lesser scaup (*Aythya affinis*), 3% canvasback (*A. valisineria*), 2%

Table 6. Average availability (%) of habitats considered suitable for nesting on study areas in the Prairie Pothole Region of Canada, 1982–85, and probability (%) that a female would select a habitat for nesting if all habitats were equally available[a]. Columns sum to 100% with rounding errors.

Habitat		Probability (%) of selection				
Class	% available[b]	Mallard	Gadwall	Blue-winged teal	Northern shoveler	Northern pintail
Cropland	16	<1	<1	<1	<1	5
Grass	16	<1	<1	14	14	<1
Brush	1	81	77	18	5	78
Wetland	4	1	<1	3	19	<1
Hayland	2	<1	2	10	25	2
Woodland	2	3	1	1	<1	<1
Right-of-way	2	10	4	39	10	12
Odd area[c]	5	4	16	16	26	2

[a] An average of 50% of landscape in all area-years was classified as Unsuitable (included area originally classified as Barren plus area of Cropland that was cultivated before early May and area of Wetland that was open water in early May or contained sparse emergent nesting cover) and not available as nesting cover.

[b] Availability is based on Table 2.

[c] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).

ruddy duck (*Oxyura jamaicensis*), 1% redhead (*Aythya americana*), 1% green-winged teal (*Anas crecca*), and <1% (2 nests) cinnamon teal (*A. cyanoptera*). Numbers of nests used for estimating survival rates, exposure periods, and estimated rates of nest success for the 5 common species are presented by habitat, study area, and year in Tables 1–5 of Appendix E.

Habitat Preference and Use for Nesting

The nesting habitat most preferred by mallards was Brush; Right-of-way was second, and lowest preference was for Cropland, Grass, and Hayland (Table 6). In parkland, we estimated that 39% of mallard nests were in Odd area, whereas in prairie, 49% of their nests were in Brush (Table 7). Proportions of mallard nests found in Right-of-way were similar in parkland (25%) and prairie (24%).

The nesting habitat most preferred by gadwalls also was Brush; Odd area was second, and lowest preference was for Cropland, Grass, and Wetland (Table 6). In parkland, we estimated that 79% of gadwall nests were in Odd area; in prairie, their nests were in relatively similar proportions in Brush (49%) and Odd area (41%) (Table 7).

Blue-winged teals preferred mostly to nest in Right-of-way; Brush was second, followed closely by Odd area and Grass (Table 6). Cropland was least preferred as nesting habitat by blue-winged teals. In parkland, we estimated that nests were ini-

Table 7. Average estimated proportion[a] (%) of nests initiated by the 5 common duck species in habitats suitable for nesting in 17 area-years[b] in the parkland and 14 area-years in the prairie, 1982–85, in the Prairie Pothole Region of Canada. Rows sum to 100% with rounding errors.

Species	Nest initiations (%)							
	Cropland	Grass	Brush	Wetland	Hayland	Woodland	Right-of-way	Odd area
Parkland								
Mallard	5	2	14	8	<1	9	25	39
Gadwall[c]	<1	1	9	<1	4	1	7	79
Blue-winged teal	<1	37	1	3	4	1	21	33
Northern shoveler[d]	<1	31	<1	12	8	<1	5	44
Northern pintail[d]	34	5	11	<1	5	<1	27	18
Prairie								
Mallard	7	1	49	5	<1	<1	24	13
Gadwall	<1	1	49	<1	3	0	9	41
Blue-winged teal[d]	<1	46	5	3	4	<1	29	14
Northern shoveler[d]	1	45	1	14	11	0	7	23
Northern pintail	45	3	31	<1	2	0	15	3

[a] Numbers of nests initiated annually in each habitat were estimated as the product of habitat composition and species preference for nesting in a habitat (Table 6), weighted by number of breeding pairs on the study area.

[b] Refers to 1 area studied for 1 year.

[c] Area-years reduced by 2 because breeding pairs were not detected on all areas each year.

[d] Area-years reduced by 1 because breeding pairs were not detected on all areas each year.

tiated by blue-winged teals in relatively similar proportions in Grass (37%) and Odd area (33%); in prairie, 46% of their nests were in Grass and 29% were in Right-of-way (Table 7).

Odd area and Hayland were both ranked high in preference for nesting by northern shovelers; Wetland was third, and lowest preference was for Cropland and Woodland (Table 6). In parkland, we estimated that 44% of northern shoveler nests were in Odd area and 31% were in Grass; in prairie, 45% of their nests were in Grass and 23% were in Odd area (Table 7). Nearly all nesting in Wetland by northern shovelers was in dry wetland basins (Table 8).

Preferences for nesting habitat by northern pintails were similar to those of mallards, except that Cropland was ranked third (Table 6). In parkland, we estimated that 34% of northern pintail nests were in Cropland and 27% were in Right-of-way; in prairie, 45% of their nests were in Cropland and 31% were in Brush (Table 7).

Chronology of Nesting

Northern pintails and mallards initiated nesting earliest of the 5 common species (Fig. 2). Mean estimates of their median nest-initiation dates did not differ ($P > 0.05$) (northern pintails = 13 May; mallards = 16 May). Blue-winged teals and northern shovelers nested later than mallards and northern pintails ($P < 0.05$). Mean estimates of their median nest-initiation dates were 28 May (blue-winged teals) and 25 May (northern shovelers) ($P > 0.05$). Gadwalls nested latest ($P < 0.05$); their mean median initiation date was 2 June.

Table 8. Number of nests of the 5 common duck species and frequency (%) of locations among upland and wetland sites in the Prairie Pothole Region of Canada, 1982–85. Rows sum to 100% with rounding errors.

		Frequency of locations		
			Wetland	
Species	n	Upland	Wet	Dry
Mallard	1,885	81	10	8
Gadwall	510	95	<1	5
Blue-winged teal[a]	995	84	1	15
Northern shoveler	616	82	2	16
Northern pintail	841	92	2	6

[a] Includes 2 cinnamon teal.

Temperature, precipitation, and availability of wet seasonal wetlands in May were correlated with median nest-initiation dates of mallards ($R^2 = 0.28$, $n = 30$, $P = 0.01$), blue-winged teals ($R^2 = 0.26$, $n = 21$, $P = 0.11$), and northern pintails ($R^2 = 0.23$, $n = 21$, $P = 0.03$). Median nest-initiation date decreased by 2.3 days for mallards ($P = 0.01$) and by 1.2 days for blue-winged teals ($P = 0.09$) per Celsius degree increase in average May temperature. Median nest-initiation date of blue-winged teals was positively related to amount of precipitation in May ($P = 0.08$). Median nest-initiation dates of mallards ($P = 0.08$) and northern pintails ($P = 0.03$) were positively related to number of wet wetlands present in May.

Average length of nest-initiation period (measured by interquartile range) did not differ ($P > 0.05$) between mallards (27 days) and northern pintails (26 days), or among gadwalls (13 days), blue-winged teals (15 days), and northern shovelers (16 days) (Fig. 2). Nest-initiation periods of the latter 3 species were shorter than those of mallards and northern pintails ($P < 0.05$).

Availability of wet wetlands in May, April–June temperature and precipitation, and nest success were correlated with length of nest-initiation period (mallards, $R^2 = 0.16$, $n = 30$, $P = 0.09$; gadwalls, $R^2 = 0.23$, $n = 15$, $P = 0.07$; blue-winged teals, $R^2 = 0.33$, $n = 21$, $P = 0.03$; northern shovelers, $R^2 = 0.44$, $n = 17$, $P < 0.01$; and northern pintails $R^2 = 0.29$, $n = 21$, $P = 0.09$). Nest-initiation period decreased by 0.29 day ($P = 0.11$) for mallards and by 0.52 day ($P = 0.08$) for northern pintails for every 1 percentage point increase in nest success. Nest-initiation period was extended by 0.10 day for mallards ($P = 0.04$) and by 0.12 day for northern pintails ($P = 0.03$) per 1.0 cm increase in May precipitation.

The nest-initiation period was extended by 0.10 day for gadwalls for every 1 percentage point increase in number of wet

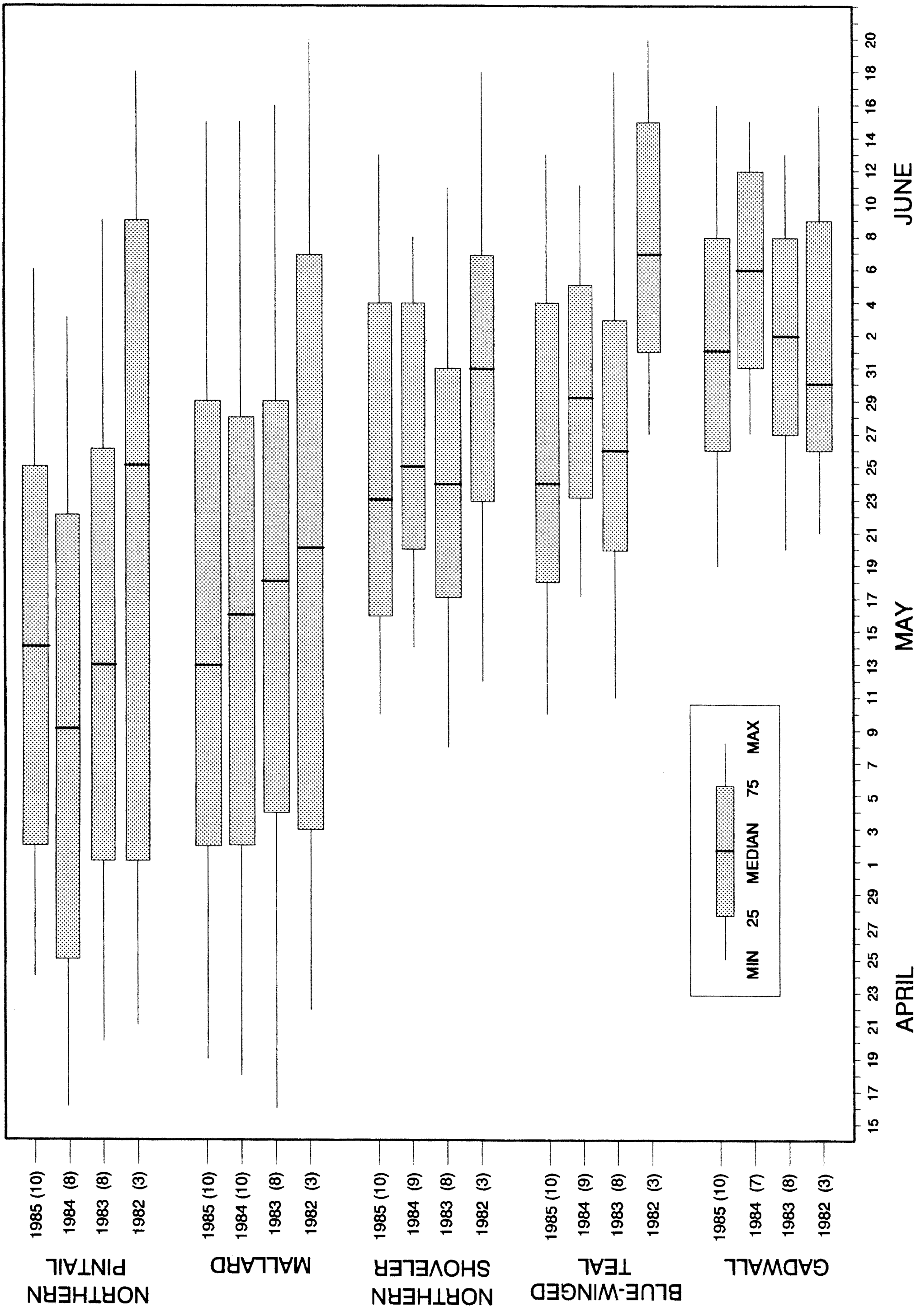

Fig. 2. Minimums and maximums, medians, and interquartiles of estimated nest-initiation dates for 5 common species of dabbling ducks in the Prairie Pothole Region of Canada. Number of study areas is in parentheses.

Table 9. Average estimates of nest success (%) by habitat and year for 5 common species of dabbling ducks combined (mallard, gadwall, blue-winged teal, northern shoveler, and northern pintail) on study areas (n) in the Prairie Pothole Region of Canada.

Year	n	Nest success (%)							
		Cropland	Grass	Brush	Wetland	Hayland	Woodland	Right-of-way	Odd area[a]
1982	3	2	19	23	18	24[b]	28[b]	10	13
1983	8	2	17	21[b]	17	15[b]	26[b]	9	11
1984[c]	10	1	8	10[b]	8	10[b]	18[b]	4	6
1985[c]	10	2	18	22[b]	19	21[b]	29[b]	10	12
$\bar{x}$		2	15	19	16	18	25	8	11

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).

[b] Nest success estimate is based on fewer than indicated number of study areas because habitat was not available on all study areas (Table 2).

[c] Nest success estimates are based on fewer than 5 species because breeding populations of some species were not detected on some study areas (Tables 1–5 of Appendix A).

wetlands present in May (P = 0.07). The nest-initiation period of blue-winged teals was extended by 0.06 day per 1.0 cm increase in May precipitation (P = 0.11) and decreased by 1.4 days per Celsius degree increase in June temperature (P = 0.04). The nest-initiation period of northern shovelers was extended by 0.13 day for every 1.0 cm increase in April precipitation (P < 0.01).

Nest Success by Species

We detected no difference (P = 0.16) in DSR's of nests among the 5 common species. Overall estimates of nest success by species were mallard (11%), gadwall (14%), blue-winged teal (15%), northern shoveler (12%), and northern pintail (7%).

Nest Success by Habitat

Nest success estimates by habitat class for all of the 5 common species combined, and averaged over all area–years, ranged from 2% in Cropland to 25% in Woodland (Table 9). Average annual estimates tended to be similar in 1982, 1983, and 1985, but were lower in 1984. We pooled our annual estimates for Grass and Brush from Table 9 and averaged them to obtain an estimate of nest success for grassland (Cowardin et al. 1988). Unweighted average annual estimates of nest success in grassland were 21% (1982), 19% (1983), 9% (1984), and 20% (1985); the average estimate for grassland was 17%. We did not compare nest success by habitat class on individual study areas because we previously excluded habitat interactions in the model used for estimating DSR's (Appendix C). We provide these estimates to demonstrate the range in nest success for various habitat categories.

Nest Success by Study Area

Nest success estimates for all species combined varied considerably among area–years (Table 10). Annual estimates were at or above the threshold level suggested for stability of mallard (Cowardin et al. 1985) and northern pintail populations (Klett et al. 1988) in 8 of 31 area–years (2 of 17 in parkland and 6 of 14 in prairie) and at or above the threshold level suggested for gadwall, blue-winged teal, and northern shoveler populations (Klett et al. 1988) in 4 area–years (1 in parkland and 3 in prairie). During 4 years on the Shamrock Study Area, estimates of nest success were at or above threshold levels for all of the 5 common species in 1982, for mallards and northern pintails in 1983, but for none of the species in 1984–85. We did not obtain an estimate of nest success as high as the threshold level for any of the 5 common species on the Hanley Study Area during 4 years of study. Average estimates of nest success overall for all area–years were near the level suggested for stability of mallard and northern pintail populations during 3 of 4 years, but below levels suggested for the other 3 common species in all 4 years.

Table 10. Estimates of nest success (%) from pooled annual averages (unweighted) for mallards, gadwalls, blue-winged teals, northern shovelers, and northern pintails on study areas in the Prairie Pothole Region of Canada.

Study area	Nest success (%) 1982	1983	1984	1985
Parkland				
Earl Grey				13
Hanley	5	10	3	12
Hay Lakes		11	12	
Holden		17		
Inchkeith			9[a]	11
Leask			12	11
Moore Park		10	9	
Penhold			5[a]	26
Yorkton				13[a]
Prairie				
Cartwright		13		
Ceylon		26	5	
Craik			4[a]	5
Denzil			4	7
Gayford				27
Goodwater		15		
Shamrock	29	15	2	13[a]
Tichfield	17			
$\bar{x}$	17	15	7	14

[a] Estimate based on <5 species because breeding population of ≥1 species was not detected.

Fates of Unsuccessful Nests

We estimated that predators destroyed 65–72% of the nests of the 5 common species (Table 11). An additional 5–6% likely failed because predators caused females to abandon nests; these nests contained ≥1 depredated egg. Pooled percentages of nests in these 2 categories indicated that 77–78% of mallard, gadwall, blue-winged teal, and northern shoveler nests and 71% of northern pintail nests failed to hatch because of predation.

We estimated that agricultural operations, mostly tillage, destroyed 17% of northern pintail nests and 2–3% of those of the other 5 common species. Nests in Cropland usually were dispersed widely, so individual tillage operations seldom destroyed many nests. However, in 1983 we found an unusually high concentration of nests (0.18/ha) in 5 fields of standing stubble on the Hay Lakes and Holden study areas during the first 2 weeks of May. The nests (46 northern pintails, 11 mallards, and 3 northern shovelers) were in 340 ha of wheat that had been cut and swathed the previous autumn, but not harvested because of deep snow; most nests were under swaths and only 5 (8%) hatched. In contrast, we found only 0.01 nest/ha (93 northern pintails, 53 mallards, 12 northern shovelers, 9 blue-winged teals, and 2 gadwalls) in all the remaining stubble fields (15,174 ha) searched during the study; 48 (28%) of these nests hatched.

We estimated that weather events destroyed 1% of nests overall. Snowstorms mainly affected early-nesting mallards and northern pintails when eggs were chilled or nests were abandoned after being buried in deep snow. Among nests known to be present on the Tichfield Study Area in 1982 during the storm of 26–29 May, 14 of 16 (88%) failed because all embryos died or nests were abandoned (10 of 11 mallards and 4 of 5 northern pintails); 8 of the 16 nests were within 4 days of hatching.

Table 11. Average estimated percentage of nests by fate and causes of failure among unsuccessful nests of the 5 common species of dabbling ducks in the Prairie Pothole Region of Canada, 1982–85. Percentages are unweighted averages of all area-years[a]. Number of area-years vary because estimates of nest success were not available for some species in some years. Rows sum to 100% with rounding errors.

			Unsuccessful (%)					
			Destroyed			Abandoned		
Species	Area-years	Successful (%)	Predation	Farm equipment	Other	Predation	Weather	Other
Mallard	31	11	72	3	<1	6	2	6
Gadwall	29	14	72	2	<1	6	1	5
Blue-winged teal	30	15	72	2	<1	5	1	6
Northern shoveler	29	12	72	2	<1	6	1	7
Northern pintail	30	7	65	17	<1	6	1	4

[a] Area-year refers to 1 area studied for 1 year.

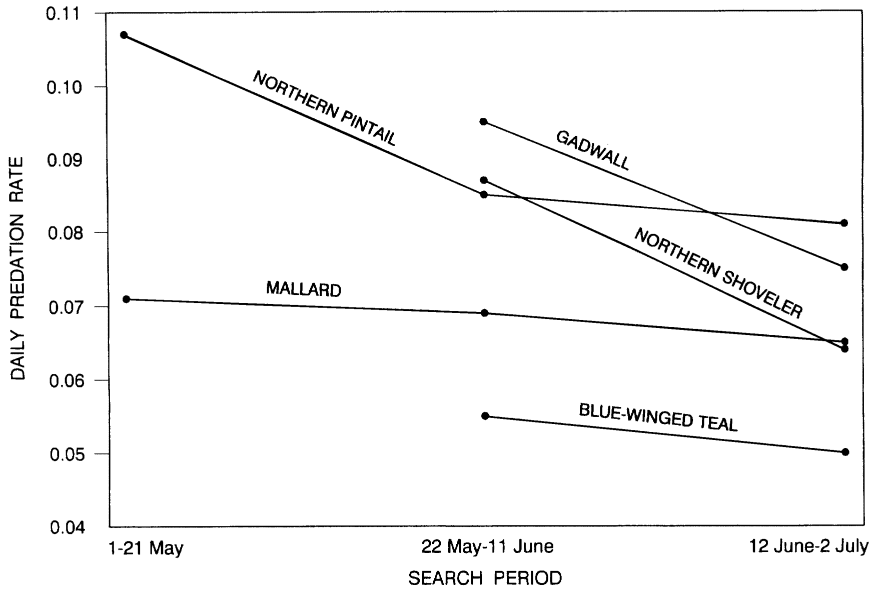

Fig. 3. Daily rates of nest predation (no. of nests destroyed or abandoned as a result of predation ÷ by no. of exposure days) by 3-week nest-search period for 5 common species of dabbling ducks in the Prairie Pothole Region of Canada combined for years 1982–85.

Among nests known to be present on the Goodwater Study Area in 1983 during the storm of 8–14 May, 16 of 77 (21%) failed as a result of the storm (9 of 43 northern pintails, 6 of 32 mallards, 1 of 1 northern shoveler, and 0 of 1 American wigeon).

Flooding from heavy rain resulted in abandonment of numerous duck nests located near or in wetlands and drainage ditches on Hay Lakes and Holden study areas in 1983. Among nests known to be present on those study areas during the storms of 18–30 June, 101 of 254 (40%) were abandoned or washed away because of flooding (27 of 61 mallards, 16 of 45 blue-winged teals, 16 of 34 lesser scaups, 19 of 22 ruddy ducks, 8 of 31 northern shovelers, 7 of 21 redheads, 1 of 9 gadwalls, 2 of 7 northern pintails, 1 of 7 canvasbacks, 1 of 5 green-winged teals, 1 of 1 cinnamon teal, and 0 of 7 American wigeons).

We found 190 nests (all species and area–years pooled) that were abandoned without evidence of egg destruction. We found dead females or their remains at 11% of these nests, but no probable cause for abandonment at the remaining.

Daily Rate of Nest Predation

Predation rates on nests of the 5 common species tended to decrease as the breeding season progressed (Fig. 3). The trend was consistent among species, but significant only for the northern shoveler ($\chi^2 = 3.85$, 1 df, $P = 0.05$). The decline in predation rates was not consistent among area–years. We detected significant interactions between area–year and search period for all species (mallard, $\chi^2 = 121.2$, 56 df, $P < 0.01$; gadwall, $\chi^2 = 39.4$, 20 df, $P < 0.01$; northern shoveler, $\chi^2 = 40.0$, 26 df, $P = 0.03$; northern pintail, $\chi^2 = 104.9$, 40 df, $P < 0.01$) except blue-winged teal ($\chi^2 = 29.7$, 23 df, $P = 0.13$). We could not explain interactions by examining annual wetness measurements. Interactions between area–year and search period were still significant for 8 of 15 categories (5 species, 3 wetness intervals) and for at least 1 species in each wetness interval. Where we did not detect interactions and where differences in nest predation rates among search periods were significant, rates were lower in later search periods.

Table 12. Summary of regressions of average estimates of nest success on percentage of Cropland[a] available on individual study areas in parkland (P) and prairie (G) of Prairie Pothole Region of Canada of the 5 common duck species, 1982–85, and predictions of mean percent of Cropland above which nest success is below threshold level[b] thought necessary for population stability.

Species	Physiographic zone	Slope	SE	t^c	*P*	Threshold	Predicted $\bar{x}$ % cropland	SE
Mallard	P	−0.119	0.090	−1.32	0.21	15	nc[d]	
	G	−0.448	0.092	−4.86	<0.01*		63	11.20
Gadwall	P	−0.083	0.131	−0.63[e]	0.54	20	nc	
	G	−0.538	0.129	−4.17[e]	<0.01*		59	13.06
Blue-winged teal	P	−0.185	0.120	−1.54	0.15	20	nc	
	G	−0.484	0.124	−3.90	<0.01*		61	13.87
Northern shoveler	P	−0.086	0.101	−0.85	0.41	20	nc	
	G	−0.342	0.110	−3.11	<0.01*		50	16.50
Northern pintail	P	−0.142	0.058	−2.45	0.03*	15	6	26.12
	G	−0.326	0.058	−5.65	<0.01*		46	10.15

[a] Based on Table 2.
[b] From Cowardin et al. (1985) and Klett et al. (1988).
[c] *t* statistic for testing of slope is equal to zero, 13 df.
[d] Not calculated because regression slope not significantly different from zero ($P > 0.05$).
[e] 12 df.
* Denotes significance ($P < 0.05$).

Nest Success and Percentage Cropland

We detected an overall effect of the percentage of Cropland present on study areas on nest success of the 5 common species (mallard—$F = 12.7$; 2, 13 df; $P < 0.01$; gadwall—$F = 8.9$; 2, 12 df; $P < 0.01$; blue-winged teal—$F = 8.8$; 2, 13 df; $P < 0.01$; northern shoveler—$F = 5.2$; 2, 13 df; $P = 0.02$; northern pintail—$F = 19.0$; 2, 13 df; $P < 0.01$). Nest success was negatively related to the percentage of Cropland present on study areas in parkland and prairie (Table 12). On study areas in parkland, we predicted nest success would be at the threshold level for population stability for northern pintails when Cropland composed 6% of the habitat present ($P = 0.03$); results for other species in parkland were not significant ($P > 0.15$). We rejected the estimate for northern pintails because the predicted value was outside the range of Cropland availability that we observed (Table 2). In prairie, however, we predicted nest success would be at threshold levels for population stability for all of the 5 common species when Cropland composed 46–63% of the habitat present. Interpretation of regression slopes indicated that on average in prairie, nest success was at threshold levels when Cropland composed 56% of the habitat present and that nest success decreased about 4 percentage points for every 10 percentage points increase in Cropland.

Mortality of Adult Ducks

We found remains of 573 dead, adult ducks on study areas during 1983–85 (Table 13). Remains were from red fox dens (20%), duck nests (13%), raptor nests (4%), roadsides (2%), and other locations (61%). We found no duck remains at coyote dens. Raptor nests with remains were those of great horned owl, red-tailed hawk, and Swainson's hawk; >95% of remains at raptor nests were on the ground.

Remains were of 7 dabbling duck and 6 diving duck species (Table 14). Dabbling ducks represented a greater proportion (94%) and diving ducks a lesser proportion (6%) of remains than expected from their proportions in the breeding population ($\chi^2 = 103.65$, 1 df, $P < 0.01$). We report only data for all years combined because annual comparisons of species found dead with those in the breeding population were nearly identical. We detected differences in proportions of individual species found dead among dabbling ducks, relative to

Table 13. Number of adult ducks from current year found dead during 1 May–5 July on all study areas in the Prairie Pothole Region of Canada by year and percentages by type of location where found. Columns sum to 100% with rounding errors.

				Total	
	1983	1984	1985	All species	Mallard
Number of ducks	185	128	260	573	240
Locations (%)					
Red fox dens	17	20	22	20	18
Duck nests	13	8	15	13	6
Raptor nests	1	15	1	4	3
Roadsides	3	2	<1	2	<1
Other locations	66	55	61	61	73

their occurrence in breeding populations ($\chi^2 = 118.94$, 6 df, $P < 0.01$), but not among diving ducks ($\chi^2 = 4.36$, 4 df, $P = 0.36$). There were nearly one-third more dead mallards and nearly twice as many dead northern pintails as expected from their relative abundance in the breeding population. Conversely, American wigeons, blue-winged teals, and northern shovelers were less abundant among dead ducks than expected.

We determined sex of 501 dead ducks (Table 15). More females than males were tallied each year among all species of dabbling ducks, except for mallards in 1984, gadwalls in 1985, and a few species for which samples were small. Disparities in the expected 50:50 ratio of females to males were significant in mallards ($\chi^2 = 20.25$, 3 df, $P < 0.01$) and northern shovelers ($\chi^2 = 8.07$, 2 df, $P = 0.02$), but not in gadwalls ($\chi^2 = 0.82$, 2 df, $P = 0.66$), blue-winged teals ($\chi^2 = 4.52$, 2 df, $P = 0.10$), or northern pintails ($\chi^2 = 5.33$, 3 df, $P = 0.15$). Among mallards, significantly more females than males were found dead in 1983 ($\chi^2 = 14.63$, 1 df, $P < 0.01$) and 1985 ($\chi^2 = 5.63$, 1 df, $P = 0.02$), but not in 1984 ($\chi^2 = 0.0$, 1 df, $P = 1.00$). Among northern shovelers, significantly more females than males were found dead in 1983 ($\chi^2 = 6.40$, 1 df, $P = 0.01$), but not in 1985 ($\chi^2 = 1.67$, 1 df, $P = 0.20$); only 10 northern shovelers were found dead in 1984.

Table 14. Numbers[a] and proportions of ducks in breeding population and of adult ducks found dead for all study areas and years combined in the Prairie Pothole Region of Canada, 1983–85.

	Breeding population		Dead ducks			
					Proportion found dead	
Species	No. counted	Proportion of dabblers or divers	No. found	Proportion	95% CL	Significance[b]
Mallard	7,136	0.316	240	0.467	0.424–0.510	>
Gadwall	2,167	0.096	40	0.078	0.055–0.101	ns
American wigeon	1,545	0.068	21	0.041	0.024–0.058	<
Green-winged teal	533	0.024	7	0.014	0.004–0.024	ns
Blue-winged teal	5,540	0.245	64	0.125	0.096–0.153	<
Northern shoveler	2,892	0.128	36	0.070	0.048–0.092	<
Northern pintail	2,801	0.124	106	0.206	0.171–0.241	>
Total dabblers	22,614	1.001	514	1.001		
Redhead	1,290	0.182	3	0.115	0.000–0.238	nt
Canvasback	942	0.133	6	0.231	0.069–0.393	nt
Lesser scaup	3,338	0.470	14	0.538	0.347–0.730	nt
Bufflehead	241	0.034	1	0.038	0.000–0.112	nt
Ruddy duck	1,290	0.182	2	0.077	0.000–0.179	nt
Total divers	7,101	1.001	26	0.999		
Dabblers	22,614	0.761	540[c]	0.942	0.923–0.961	>
Divers	7,101	0.239	33[d]	0.056	0.039–0.077	<
Total ducks	29,715	1.000	573	0.998		

[a] Summed across 1983, 1984, and 1985.
[b] Notation implies that proportion of the dead ducks for an individual species is significantly greater than (>), significantly less than (<), or not significantly different from (ns) the proportion of that species in the breeding population, or that no test was conducted (nt) because overall chi-squared test was not significant. Significance level used was $P < 0.05$.
[c] Includes ducks identified to dabbler, but not to species.
[d] Includes ducks identified to diver, but not to species.

Table 15. Number of ducks found dead, number identified to sex, and percentage of females among those identified to sex for all study areas combined by year in the Prairie Pothole Region of Canada.

	1983			1984			1985			Total		
Species	No. found	Sex known	% female	No. found	Sex known	% female	No. found	Sex known	% female	No. found	Sex known	% female
Mallard	78	70	72.9	69	62	50.0	93	86	62.8	240	218	62.4
Gadwall	11	11	63.6	6	6	100.0	23	22	50.0	40	39	61.5
American wigeon	14	11	63.6	2	1	100.0	5	5	80.0	21	17	70.6
Green-winged teal	2	2	50.0	1	1	0.0	4	4	75.0	7	7	57.1
Blue-winged teal	16	15	73.3	6	6	83.3	42	39	59.0	64	60	65.0
Northern shoveler	14	10	90.0	6	4	75.0	16	15	66.7	36	29	75.9
Northern pintail	40	37	59.5	20	19	63.2	46	45	62.2	106	101	61.4
Unknown dabbler	5	1	0.0	10	1	100.0	11	4	100.0	26	6	83.3
Total dabblers	180	157	68.8	120	100	59.0	240	220	62.3	540	477	63.7
Redhead	0			0			3	3	67.7	3	3	66.7
Canvasback	1	1	0.0	0			5	5	60.0	6	6	50.0
Lesser scaup	3	3	33.3	5	4	50.0	6	4	75.0	14	11	54.6
Bufflehead	0			1	1	0.0	0			1	1	0.0
Ruddy duck	1	1	0.0	1	1	100.0	0			2	2	50.0
Unknown diver	0			1	0		6	1	100.0	7	1	100.0
Total divers	5	5	20.0	8	6	50.0	20	13	69.2	33	24	54.2
Total ducks	185	162	67.3	128	106	58.5	260	233	62.7	573	501	63.3

Cause of mortality seldom could be determined because dead ducks were represented mostly by scattered feathers or feathered body parts, but predators were strongly implicated. Nearly all dead ducks had been fed on by predators, and nearly all fresh carcasses that we examined had predator-inflicted wounds with recent hemorrhaging; all dead females found at nests showed evidence of predation. No other causes of mortality were indicated except for a few ($n = 11$) collisions with vehicles or overhead wires. We observed 22 instances of raptors killing ducks or feeding on fresh duck carcasses—10 by Swainson's hawks, 9 by northern harriers, and 1 each by a ferruginous hawk, falcon (species unknown), and great horned owl.

The incidence of dead female mallards in relation to size of breeding populations on individual study areas provided insight into the extent of mortality that occurred. We found an average of 0.27, 0.14, and 0.22 dead mallard females/km^2 on all study areas during 1983–85, respectively. Based on annual breeding population estimates of 8.3, 3.7, and 3.2 mallard females/km^2 (Table 1 of Appendix A), we estimated that 3.3, 3.7, and 6.9% of available female mallards were found dead during 1983–85, respectively.

Components of Mallard Production

Data were available for 49 of the 56 half-area–years studied during 1983–85. The west half of the Yorkton Study Area in 1985 was omitted because pairs were counted on only part of the area; the 6 others were excluded because no hatched nests were found on them. Correlations between log(Hatched Nests) and the 4 variables on the right-hand side of equation (4) were as follows:

log(Wetlands)

$$r = 0.27 \quad (P = 0.06),$$

log(Pairs/Wetland)

$$r = 0.13 \quad (P = 0.38),$$

log(Nests/Pair)

$$r = 0.37 \quad (P = 0.01),$$

log(Hatched nests/Nest)

$$r = 0.57 \quad (P = 0.0001).$$

Thus, of these 4 variables, the one that most closely correlated with the number of hatched nests was the nest success rate, followed by a measure of the nesting effort, and then by the number of wet wetlands. The density of mallard pairs per wetland was not significantly correlated with Hatched Nests.

If the alternate model described by equation (5) is fitted, correlations between log(Hatched Nests) and the constituent variables are as follows:

log(Pairs)

$$r = 0.47 \quad (P = 0.0007),$$

log(Nests/Pair)

$$r = 0.37 \quad (P = 0.01),$$

log(Hatched nests/Nest)

$$r = 0.57 \quad (P = 0.0001).$$

In this formulation, the nest success rate is still the most influential, but is followed closely by the number of pairs, and then by the measure of nesting effort.

Geographic and Temporal Effects on Mallard Production

We detected a significant interaction between year and study area for temporary wetlands and seasonal wetlands among pooled results from areas studied in 1983 and 1984 or 1984 and 1985 (Table 16), indicating that drought did not affect each study area similarly in all years. Temporary wetlands were highly variable (both geographically and annually), seasonal wetlands were less variable than temporary ones, and semipermanent wetlands were even less variable. Temporary wetlands were about equally variable from year to year as among areas, as indicated by the ratios of their CV's (CV_Y/CV_{SA} = 0.91). Seasonal wetlands were more variable year to year than among areas (CV_Y/CV_{SA} = 1.49). As expected from their greater permanence, semipermanent wetlands varied less from year to year than among areas (CV_Y/CV_{SA} = 0.49).

Pairs were moderately variable, and equally so among years and areas (CV_Y/CV_{SA} = 0.95). Nest success also was moderately variable, but somewhat more so among years than areas (CV_Y/CV_{SA} = 1.69).

DISCUSSION

Nest success of the common species was generally low on most areas we studied during 1982–85. Based on suggested threshold rates for stability (Cowardin et al. 1985, Klett et al. 1988), we believe that breeding populations of these species were not self-sustaining in many area–years. Our results are similar to those of other recent studies (Table 17) (Cowardin et al. 1985, Johnson et al. 1987, Klett et al. 1988). These findings suggest that many areas of the PPR of North America are not producing sustainable populations of dabbling ducks.

Because we focused on areas of high mallard densities, our results may not apply generally to the entire Canadian PPR. The relatively high breeding populations of mallards on areas we selected for study suggest that adequate numbers of wetlands were present to support duck populations. Many of our study areas also contained relatively large tracts of native prairie grassland that sometimes was contiguous with an adjacent area of grassland. Ducks associated with large grasslands may have benefited from factors such as relatively favorable predator communities (e.g., dominated by coyotes) (Sovada et al. 1995) and stable amounts of upland vegetation for nesting. If our results are biased because we focused on areas where mallard populations were high and habitat conditions favored duck protection, then we believe they are biased toward the best remaining areas of this important breeding ground, and large portions of this area of Canada may be less suitable for nesting ducks than we observed.

Factors Related to Duck Production

Habitat Composition and Use.—Habitat composition of the PPR has changed dramatically in the past 100 years. Much

Table 16. Statistics associated with variance components of factors involved in mallard production: mean, variance components, and coefficients of variation (CV = square root of variance component divided by mean).

Dependent variable	Mean	Variance component				CV (%)		
		Error	Study area	Year	Study area times year	Error	Study area	Year
Temporary wetlands[a]	7.97	22.39	51.55	43.37	46.11	59	90	82
Seasonal wetlands[a]	19.39	156.73	83.21	184.81	175.31	64	47	70
Semipermanent wetlands[a]	16.01	86.83	46.98	11.04	0[b]	58	43	21
Mallard pairs	62.58	611.93	547.87	470.74	0[b]	40	37	35
Nest success rate	0.1034	0.0047	0.0007	0.0021	0[b]	81	26	44

[a] Wetlands refer to those that contained visible standing water in May.
[b] Variance component not significantly different from zero.

of the Region is now less suitable for duck production than it once was. Fewer wetlands hold water because of drainage, and large expanses of upland are tilled annually in both the parkland and prairie of Canada (Bird 1961, Lynch et al. 1963, Kiel et al. 1972, Archibold and Wilson 1980, Sugden and Beyersbergen 1984). Lynch (1984) suggested that duck production in the PPR is a boom-or-bust phenomenon, with variability greatest in prairie where dramatic annual changes in weather affect habitat conditions. Lynch et al. (1963) suggested that conditions leading to high duck production might have occurred in 4 or 5 years out of 10 under pristine conditions, but in only 2 or 3 years out of 10 where habitats have now been altered by agriculture.

Large portions of all areas we studied were extensively altered through cultivation, and some areas had many drained wetlands. Most dabbling duck nests we found in extensively cultivated areas were in the scattered patchwork of vegetation that remained along roads, fences, and around wetlands. Some nests were in wetlands and hayfields, but very few were in grain stubble, except those of northern pintails. Conversely, large pastures where agricultural activities were limited to grazing were especially important to dabbling ducks. Eight study areas had large (>2.6 km^2) pastures that were contiguous with additional pastureland adjacent to the study area; the largest contiguous area of pasture (92 km^2) was associated with the Ceylon Study Area. Nest success on individual study areas was positively correlated with amount of pasture available on the study area (Greenwood et al. 1987).

Ducks used habitats for nesting similarly

Table 17. Nest success estimates (%) by habitat class for dabbling ducks in the Prairie Pothole Region of North America.

Study	Year and location	Species	Nest success (%)						
			Cropland	Grazed grassland	Hayland	Planted cover	Wetland	Right-of-way	Odd area[a]
Cowardin et al. (1985)	1977–80; N.D.	mallard	<1	12	7	na[b]	7	3	11
Johnson et al. (1987)	1983; N.D., S.D., Mont.	dabbling ducks	3	13	22	19	10	6	10
Klett et al. (1988)	1966–84[c]; N.D., S.D., Minn.	5 common species[d]	6	14	10	13	14	9	4
Present study	1982–85; Alta., Sask., Manit.	5 common species[d]	2	17[e]	18	na	16	8	11

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).
[b] Habitat class not available.
[c] We pooled the annual estimates for all species for period 1980–84 in N.D. and calculated the average, weighted by annual estimated number of nests initiated.
[d] Mallard, gadwall, blue-winged teal, northern shoveler, and northern pintail.
[e] We pooled our annual estimates for our classes Grass and Brush and calculated the overall average for all years.

to previous reports. Many northern pintails and some mallards nested in stubble fields (Milonski 1958, Higgins 1977, Cowardin et al. 1985). Our estimates of nest initiations in Cropland were based on searches of untilled stubble and thus may be low. At more southern latitudes, growing grain provides some suitable habitat for nesting ducks (Higgins 1977, Duebbert and Kantrud 1987). At the latitude of our study, however, spring-seeded grain provided little cover for nesting until mid- to late June, and we had no fields of fall-seeded grain that Duebbert and Kantrud (1987) found to be important to dabbling ducks. Although change in tillage practices might attract more ducks to nest in cropland and reduce mechanical destruction of nests (Cowan 1982, Rodgers 1983, Duebbert and Kantrud 1987), such changes may do little to reduce predation, which we found to be the primary cause of nest failure.

Use of native grassland by nesting ducks and the importance of Brush have been well documented in the PPR (e.g., Keith 1961, Salyer 1962, Smith 1971, Stoudt 1971, Cowardin et al. 1985, Duebbert et al. 1986, Sugden and Beyersbergen 1987). Smith (1971) suggested that brush was used more for nesting in dry years (when grass was scant) than in wet years. However, we found several species used brush during both wet and dry years; Cowardin et al. (1985) observed the same with radio-equipped mallards in North Dakota.

Use of dry wetlands for nesting that we observed by blue-winged teals and northern shovelers has been reported earlier (Bellrose 1980, Klett et al. 1988), but, as we found, mallards were the only dabbling ducks to commonly nest over water (Jessen et al. 1964, Krapu et al. 1979, Bellrose 1980, Arnold et al. 1993). In 1984, the driest year of our study, 30% of all nests of the 5 common species were in Wetland compared to 3% in 1982, 13% in 1983, and 12% in 1985. Extent of nesting in dry wetlands in 1984 may reflect diminished attractiveness of upland vegetation during drought, or the attractiveness of often rank cover in dry wetland basins.

Odd area and Right-of-way contained 45–86% of the nests of the 5 common species in parkland and 18–50% in prairie. High proportions of nests in these habitats, especially in parkland, probably reflect the shortage of more preferred nesting habitats in areas where Cropland was abundant. Klett et al. (1988) reported that Odd area and Right-of-way contained 6–25% of the nests of the 5 common species during 1980–84 in North Dakota, South Dakota, and Minnesota.

We found few nests in Hayland, although alfalfa is frequently used by nesting ducks, especially mallards and blue-winged teals (Salyer 1962, Ordal 1964, Evans and Wolfe 1967, Cowardin et al. 1985). Many of our study areas contained little Hayland, especially alfalfa, and drought may have reduced its attractiveness. Cowardin et al. (1985) found alfalfa to be most used by nesting mallards when it was relatively tall.

Scant information on nesting in Woodland is available to compare to our findings. However, a recent study in Alberta showed that radio-equipped mallards regularly nest in Woodland (D. W. Howerter, Ducks Unlimited Canada, Winnipeg, Manit., pers. commun.).

Proportion of Land in Cultivation.— An average of 59% of the land on our study areas was Cropland, but elsewhere in the Canadian PPR the proportion of land tilled annually may be considerably higher. Lynch et al. (1963) estimated that by the mid-1950's, 72% of the grassland in Canada was farmed for grain production. Sugden and Beyersbergen (1984) reported that in 1982, 78% of the parkland in east-central Saskatchewan was tilled annually. Areas of upland and wetland continue to be converted to cropland, especially small woodlots and pastures, margins around wetlands, and road rights-of-way (Adams and Gentle 1978, Sugden and Beyersbergen 1984, Boyd 1985, Turner et al. 1987). Boyd (1985) suggested that this trend toward farming "marginal" land (much of which we classified as Odd area) poses a greater threat to ducks than changes on the best agricultural land, which is already under cultivation.

We found that nest success on study areas in prairie was negatively correlated with proportion of land cultivated annually and decreased about 4 percentage points for every 10 percentage points increase in amount of Cropland. Because few ducks (except northern pintails) nested in Cropland, nest success in other habitats apparently decreased as amount of Cropland increased. The higher preference of northern pintails for nesting in Cropland may render that species more sensitive than others to amount of Cropland that is present.

We believe that nests are at higher risk to destruction in small blocks of upland nesting habitat than are nests in large contiguous blocks that have not been fragmented by cultivation. This is supported by our finding that nest success estimates in Odd area and Right-of-way, both common habitats of fragmented landscapes, were among the lowest estimates we obtained for all habitats, except Cropland. Higgins (1977) suggested that upland-nesting ducks cannot sustain breeding populations where ≥85% of the land is cultivated annually. In our study, the threshold appeared to be considerably lower. We suggest, however, that caution be exercised in directly applying our predicted values elsewhere because of the conditions of drought under which our study was conducted.

Weather.—Weather events, especially spring snowstorms and flooding, had direct negative effects on nest success on some study areas. However, the more general influence of weather on duck production probably occurred indirectly through effects on habitat conditions, particularly wetland habitat. Local wetlands provide most nutrients needed by females for egg production, especially for renesting (Krapu 1974, 1979, 1981; Swanson et al. 1979; Krapu et al. 1983). Renesting is particularly important to annual production of ducks when success of initial nesting attempts is low (Gates 1962, Pospahala et al. 1974, Swanson et al. 1979).

We found that initiation date and length of nest-initiation period were related to temperature, availability of wet wetlands in May, and amount of precipitation during nesting season, but it is unclear which factors had greatest influence. Below average temperatures in early spring may delay nest initiation (Sowls 1955:85, Smith 1968, Hammond and Johnson 1984, Cowardin et al. 1985), and above-average temperatures later in the nesting season may cause ducks to terminate nest initiation (Dzubin and Gollop 1972). Abundant wet wetlands and ample precipitation both are likely to enhance the potential for renesting (Krapu 1979, Swanson et al. 1979, Hammond and Johnson 1984, Cowardin et al. 1985, Swanson et al. 1985). Crissey (1969) found a positive relationship between annual production of mallards on a continental basis and number of wet wetlands present in July in the PPR of Canada; that finding suggests that production is highest when conditions for renesting and brood survival are good. Krapu et al. (1983) and Jackson et al. (1985) noted reduced mallard nesting activity and duration during drought. Krapu et al. (1983) observed that females abandoned breeding sites and had smaller home ranges and that a high percentage of radio-marked females did not nest during drought. Duncan (1987), who studied northern pintails in southern Alberta in 1984, found virtually no renesting during that drought year.

We found that predation rates tended to decrease as the nesting season progressed, similar to Sugden and Beyersbergen (1986), who found less predation on artificial nests in late June and July than earlier in the season. Although we had no direct evidence of cause for this, we believe that seasonal changes in availability of buffer prey and in habitat conditions both may have affected nest success. Abundance of buffer prey is known to affect predation rates on birds and eggs in other ecosystems (Larson 1960, McInvaille and Keith 1974, Pehrsson 1986, Summers 1986, Beintema and Müskens 1987). As upland nesting cover becomes more dense with seasonal growth, better concealed and more dispersed nests also may reduce the foraging efficiency of some predators. Although higher nest success has been reported in dense cover (Kirsch et al. 1978; Livezey 1981; Cowardin et al. 1985; Sugden and Beyersbergen 1986, 1987), a recent review by Clark and Nudds (1991) did not clearly confirm or refute the reported benefits of dense nesting cover. Clark and Nudds (1991) suggested that amount of concealment of nests was important to survival of duck nests in the PPR only when predation was predominantly by birds.

Our findings suggest that currently there is an advantage to ducks that nest later in the season because of higher nest success then; females that initiate nesting later also may be less vulnerable to predation (*see* Mortality of Adult Ducks). To benefit from higher hatch rates later in the nesting season, early-nesting species such as the mallard and northern pintail must delay initial nesting or be able to renest when initial nests are destroyed, whereas later-nesting species such as the gadwall, blue-winged teal, and northern shoveler may benefit more regularly. Selection might favor mallards and northern pintails that successfully nest for the first time later in the season. This selective force would be even stronger if mortality of nesting females from predation was reduced by delayed nesting (Rohwer 1992). There also are disadvantages to nesting late, however, including declines in clutch size, renesting potential, and brood survival rates that must be balanced against the apparent advantages (Rohwer 1992).

Unless success of initial nests is high, the cumulative effects of drought appear to result in an overall reduction in the average nest success rate and, ultimately, in lower hen success. Renesting, which is important to hen success, depends on quality of wetland habitat (Krapu 1979; Swanson et al. 1979, 1985; Cowardin et al. 1985). Annual estimates of nest success are derived from total nests observed throughout the nesting season. If the nesting season is truncated because of high temperatures, reduced precipitation, or deteriorating wetland conditions, the potential for renesting will be reduced. Thus during drought, contributions to annual estimates from nests initiated in the later portion of the nesting period are lost; it is then that success tends to be highest. Drought likely increased the severity of our low estimates of nest success in some area–years through effects on renesting.

Predator Community.—Johnson et al. (1989) used data from our study to examine the relation of individual egg-eating predator species to nest success. They found that daily predation rates on nests of the 5 common species were positively related to activity indices of 6 mammals (coyote, red fox, raccoon, striped skunk, badger, and Franklin's ground squirrel) and 2 birds (American crow and black-billed magpie). They concluded that the red fox was the most influential predator on duck nests on our study areas. Activity indices of the red fox were positively related ($P < 0.01$) to predation of both early nests (initiated during first or second nest-search periods) and late nests (initiated during third nest-search period). Activity indices of American crows ($P < 0.01$) and badgers ($P < 0.10$) were positively related to predation on early, but not late nests. Activity indices of striped skunks were positively related ($P < 0.10$) to predation on late nests only. Neither Franklin's ground squirrels nor black-billed magpies were strongly implicated in predation on our duck nests, but Johnson et al. (1989) suggested they were locally important.

Johnson et al. (1989) also detected a strong negative relation between red fox and coyote activity indices ($r = -0.51$, $P < 0.01$), consistent with the spatial avoidance and agnostic behavior between these 2 species (Voigt and Earle 1983, Sargeant et al. 1987). A similar avoidance relationship may have influenced the distribution of coyotes and raccoons ($r = -0.11$, $P < 0.01$; Johnson et al. 1989) and red-tailed hawks and American crows (Sargeant et al. 1993). Such interactions, which appear to be only partly related to habitat, greatly complicate evaluation of relations between duck nest success and habitat because they tend to obscure habitat effects. Sovada et al. (1995) found in areas of similar habitat, for instance, that nest success of dabbling ducks averaged 15 percentage points higher in areas occupied by coyotes than in areas occupied by red foxes.

Causes of Nest Failure

The high rate of nest failure due to depredation of clutches that we observed is consistent with other recent investigations in the PPR (Higgins 1977, Cowardin et al. 1985, Greenwood 1986, Johnson et al. 1987, Klett et al. 1988). Besides nests that failed directly because of predation on eggs, we believe many nests that were abandoned without evidence of egg destruction also failed because predators, especially raptors, killed attending females; this is indicated by our finding of female carcasses at 11% of 190 nests abandoned without evidence of egg destruction (*See* Mortality of Adults). Large raptors are known to prey on adult ducks (McInvaille and Keith 1974, Schmutz et al. 1980), but few raptors that eat eggs were present on our study areas (Sargeant et al. 1993). An exception is the northern harrier, which occasionally preys on hatching eggs (Willms and Kreil 1984).

Farming activities were not a major source of nest failure except for northern pintails; few other species nested in Cropland and there were few nests in Hayland. We did not observe nest destruction in Right-of-way and dry Wetland by mowing that occurred on most study areas in late June. Had our study been conducted during wetter years more favorable to renesting, we might have found mowing to be a greater cause of nest failure. Mowing has been shown to cause much nest destruction and female mortality in other studies (Ordal 1964, Evans and Wolfe 1967, Cowardin et al. 1985).

Weather events, likewise, were not a major cause of nest failure, although storms were important locally. Snowstorms caused embryo mortality and nest abandonment, especially among mallards and northern pintails. Although embryos can survive limited exposure to subfreezing temperatures (Greenwood 1969, Batt and Cornwell 1972), Dzubin and Gollop (1972) reported that chilling of embryos during cold spring weather was partly responsible for failure of up to 9% of eggs in early mallard nests. Johnson et al. (1986) suggested that nest failure due to spring snowstorms may be compensated by renesting due to improved wetland conditions. Storms also may benefit nesting ducks by delaying cultivation, but Milonski (1958) and Krapu (1977) speculated that ducks might not benefit if such delay only postpones nest destruction until a later date when conditions may be less favorable for renesting. Reduced availability of aquatic invertebrates that are consumed by laying females also may occur after snowstorms and influence nesting (Krapu 1979, Swanson et al. 1979). Dane and Pearson (1971) reported that mallards and northern pintails ceased laying during a severe spring snowstorm.

Flooding destroyed duck nests on the Hay Lakes and Holden study areas in 1983, but was of little consequence elsewhere. Flooding on these study areas was aggravated by drainage; ditches that connected wetlands appeared to accelerate movement of run-off water among basins and cause low-lying areas to flood rapidly. Johnson et al. (1986) suggested that flooding in mid-May should have only minor influence on mallards because renesting would compensate for losses. We found that flooding in June, however, caused the failure of nearly 50% of the nests of mallards that were probably renesting, and also numerous nests of late-nesting species, such as the lesser scaup and ruddy duck, which are not prone to renest (Bellrose 1980).

Mortality of Adult Ducks

Dead ducks whose remains we collected probably represent only a small portion of the actual number of ducks that died on our study areas (Sargeant et al. 1984, Murphy 1993). Remains often were inconspicuous and easily overlooked, and we visited study areas only at widely spaced intervals. It is not surprising that we found no duck remains at coyote dens; adult coyotes feed their young mostly by regurgitation of food consumed elsewhere (Bekoff 1977). Some raptors may be more strongly implicated than we determined; we examined <10% of the raptor nest bowls for food remains. Based on locations and types of recovery sites, observations of feeding predators, abundance of predator species, and published accounts (McInvaille and Keith 1974, Schmutz et al. 1980, Sargeant and Arnold 1984), we believe the red fox, coyote, northern harrier, Swainson's hawk, red-tailed hawk, and great horned owl were most strongly implicated in mortality of adult ducks. Although mink also are major predators of adult ducks in the PPR (Eberhardt 1973, Eberhardt and Sargeant 1977), they probably were of little consequence during our study because they were absent from most study areas during drought (Sargeant et al. 1993).

We believe mallards and northern pintails were most abundant among dead ducks in relation to breeding populations because they begin nesting earlier than other dabbling ducks when nesting cover and prey often are scant. We interpret the preponderance of females among dead ducks to reflect their heightened vulnerability to predation during nesting. Sowls (1955:117) suggested that mortality of nesting females ducks may contribute to imbalanced sex ratios in breeding populations. Johnson and Sargeant (1977) demonstrated that mortality of nesting female mallards could explain imbalanced sex ratios common in that species (Bellrose et al. 1961). Mallard females in our study easily could have experienced the 20–30% mortality rate reported in North Dakota (Johnson and Sargeant 1977, Cowardin et al. 1985) or the 40% mortality rate in the PPR of Canada and Minnesota during the present study (Blohm et al. 1987).

Mallard Production

Variation in Components.—Nest success rate appeared to be the most influential factor in determining annual production of mallards, as indexed by numbers of successful nests. The size of the breeding population also was strongly influential, although its 2 constituents, number of wet wetlands and number of mallard pairs per wetland, individually did not relate strongly to production. A measure of nesting effort (estimated nests per pair) was significantly related to production as well. Despite shortcomings in some methods we used to estimate some values, this analysis clearly shows for a variety of areas studied in several years that nest success rate is the most influential component of reproduction among the components we measured. This finding is consistent with conclusions reached in several other studies in the PPR (e.g., Cowardin and Johnson 1979, Cowardin et al. 1985, Johnson et al. 1986, Klett et al. 1988, Johnson et al. 1992).

Geographic and Temporal Factors.—A major finding from this analysis is the considerable variability in estimated values of variables associated with mallard production. Geographic variation was high, temporal variation was high, and the unexplained variation was high. This last term is often called "error variance" because it reflects the difference between observed values and those predicted by some model. Estimated components of variance due to error exceeded those due to geographic and temporal variability for all factors except temporary wetlands. In the present instance, a large error variance suggests that the variable of interest, such as number of wet wetlands or nest success rate, does not depend solely on the study area and year, but that it also varies in response to other factors. Some of the other factors that may be responsible for this high error variance were discussed earlier (e.g., availability of buffer prey, changes in habitat conditions, and habitat fragmentation).

The interaction between study areas and years for temporary and seasonal wetlands is further evidence that drought, as it affected these 2 wetland counts, was not manifested equally across the PPR of Canada, but affected different areas at different times. The finding that semipermanent wetlands varied less among years than among areas is not surprising in view of their considerable persistence from year to year.

Numbers of mallard pairs varied less than numbers of wet wetlands of any class, which suggests that mallard numbers are not as volatile as wetland conditions and that mallards respond to factors other than numbers of wet wetlands (e.g., philopatry) when settling their breeding habitat.

Our finding that nest success was more variable among years than among areas was somewhat surprising, because predation was the cause of most nest failures and indices for many predator species varied considerably from area to area, but varied little among years (Sargeant et al. 1993). Clearly predator numbers were not the sole determinant of the nest success (Johnson et al. 1989). Other factors, such as the abundance of buffer prey, may have contributed substantially to temporal variation. In addition, predation rates were related to weather variables as indexed by the wetland counts, which did vary temporally.

CONCLUSIONS

1. On most of our study areas in the PPR of Canada during 1982–85, native habitats used by ducks for nesting were extensively reduced in amount and fragmented because of prior clearing and cultivation.
2. Annual estimates of nest success were at or above suggested threshold levels for maintaining stable populations (15%) for mallards and northern pintails in 8 of 31 area–years and (20%) for gadwalls, blue-winged teals, and northern shovelers in 4 of 31 area–years.
3. Approximately 77% of all nests initiated failed directly because of predation. Although predation was the overwhelming cause of nest failure, predator numbers did not appear to be the sole determinants of predation. Predation rates were related to weather variables and other factors that may have strongly affected nest success (possibly abundance of buffer prey and extent of fragmentation of nesting habitat).
4. Large pastures in native grassland were probably the most productive areas for upland-nesting ducks. Productivity was related to size of pasture, amount of brush, and mammalian predator community. Large pastures were remote and had few roads and infrequent visitors—all factors that probably contributed to habitation by coyotes.
5. Nest success was negatively correlated with amount of cropland present and decreased about 4 percentage points for every 10 percentage points increase in amount of cropland. Under conditions of our study in the prairie physiographic zone, we predict that the 5 common species cannot maintain local breeding populations where cropland exceeds about 56% of the habitat.
6. In areas where cropland is abundant, nesting habitat usually is in fragmented tracts that tend to be occupied by a mammalian predator community dominated by red foxes.
7. Warm weather, precipitation, and abundant wet wetlands in April and May promoted early nest initiation. Length of nest-initiation period was extended by precipitation during the nesting season, but high rates of nest success and above average temperatures tended to shorten it.
8. Ducks initiating nests toward the end of the breeding season tended to suffer lower rates of nest predation than earlier nesters, which imparted an advantage to renesting ducks and late-nesting species.
9. Relatively high mortality of ducks, especially females, occurred during the breeding season due to predation, most likely by red foxes, coyotes, northern harriers, Swainson's hawks, red-tailed hawks, and great horned owls. Mallards and northern pintails were especially abundant among dead ducks because they nested early when other prey likely were scant. Females were more vulnerable to predators during the breeding season than were males because females tended the nest. Many abandoned nests, at which we found

no evidence of egg destruction, were probably due to death of the female.

10. Nest success rate, as indexed by the number of successful nests, appeared to be the most influential factor in determining mallard production. Size of the breeding population also was strongly influential.
11. Nest success varied geographically, annually, and in response to other unidentified factors. Components of variance associated with unexplained variation exceeded those associated with either geographic or temporal variation for all variables, except for number and extent of temporary wetlands.
12. Large areas of the PPR in Canada presently are not producing the sustainable populations of dabbling ducks for which this Region was known in past decades. Although we believe our study areas represent habitat conditions across the PPR of Canada, it is possible conditions on our study areas were better for duck production than other parts of the Region. If our study areas represent the best areas for duck production, then much of this important breeding ground probably is less suitable for nesting ducks than we observed.

MANAGEMENT AND RESEARCH RECOMMENDATIONS

1. Large tracts of grassland that remain in the PPR should be protected from cultivation and other manipulation (e.g., pasture "improvement" through elimination of brush) that would reduce their value to nesting ducks.
2. Nest success, habitat composition, and predator populations should be assessed periodically throughout the PPR to provide current information for management decisions. Change from a predator community dominated by red foxes to one dominated by coyotes can result in marked changes in productivity of ducks.
3. Management efforts to increase duck production need to consider habitat and predator effects simultaneously. Management applied at the landscape level (e.g., restoration of wetlands, planting of upland nesting cover) likely will be most effective in increasing duck production when conducted in regions where nest success is highest. Management applied at the local level (e.g., erection of predator barriers, intensive predator management) may be more appropriate in regions where nest success is low. Some management (e.g., restoration of wetlands, planting isolated fields of upland nesting cover) applied where nest success is low actually may be counterproductive by drawing ducks to areas where there is low probability they will nest successfully and where they otherwise may not have settled.
4. Management to protect coyotes in sufficient numbers to exclude red foxes should be encouraged where possible in areas suitable for duck production in the PPR. Population densities at which coyotes are most favorable to nesting ducks without inflicting unacceptable damage to livestock and other desirable wildlife species should be determined.
5. Research should address the relations among predator community composition, predator abundance, habitat type, block size, and duck nest success. Estimates of variability in duckling survival rates, in addition to nest success rates, are needed to more accurately predict effects of management applications on duck populations.

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Received 19 August 1992.
Accepted 20 August 1994.

APPENDIXES

Appendix A, Table 1. Estimated density (pairs/km²) of breeding mallards on study areas ($\bar{x}$ = 26.8 km²) in the Prairie Pothole Region of Canada.

Study area	Density of pairs[a] 1982	1983	1984	1985
Parkland				
Earl Grey				3
Hanley	7	7	3	5
Hay Lakes		13	10	
Holden		10		
Inchkeith			1	3
Leask			3	3
Moore Park		8	5	
Penhold			2	3
Yorkton				5
$\bar{x}$	7	10	4	4
Prairie				
Cartwright		3		
Ceylon		8	2	
Craik			2	2
Denzil			4	2
Gayford				3
Goodwater		9		
Shamrock	5	7	3	3
Tichfield	4			
$\bar{x}$	5	7	3	3
Overall $\bar{x}$	6	8	3	3

[a] Extrapolated from counts provided by Off. Migr. Bird Manage., U.S. Fish and Wildl. Serv., Laurel, Md.

Appendix A, Table 2. Estimated density (pairs/km²) of breeding gadwalls on study areas ($\bar{x}$ = 26.8 km²) in the Prairie Pothole Region of Canada.

Study area	Density of pairs[a] 1982	1983	1984	1985
Parkland				
Earl Grey				1
Hanley	2	1	<1	2
Hay Lakes		2	2	
Holden		1		
Inchkeith			1	<1
Leask			1	2
Moore Park		1	1	
Penhold			0	<1
Yorkton				0
$\bar{x}$	2	1	1	1
Prairie				
Cartwright		1		
Ceylon		7	2	
Craik			2	1
Denzil			2	1
Gayford				2
Goodwater		2		
Shamrock	1	2	2	1
Tichfield	1			
$\bar{x}$	1	3	2	1
Overall $\bar{x}$	2	2	1	1

[a] Extrapolated from counts provided by Off. Migr. Bird Manage., U.S. Fish and Wildl. Serv., Laurel, Md.

Appendix A, Table 3. Estimated density (pairs/km²) of breeding blue-winged teals on study areas ($\bar{x}$ = 26.8 km²) in the Prairie Pothole Region of Canada.

Study area	Density of pairs[a] 1982	1983	1984	1985
Parkland				
Earl Grey				2
Hanley	<1	1	1	5
Hay Lakes		9	8	
Holden		8		
Inchkeith			<1	3
Leask			5	7
Moore Park		7	7	
Penhold			1	<1
Yorkton				4
$\bar{x}$	<1	6	4	4
Prairie				
Cartwright		2		
Ceylon		6	3	
Craik			1	2
Denzil			4	6
Gayford				3
Goodwater		6		
Shamrock	3	6	1	0
Tichfield	2			
$\bar{x}$	2	5	3	3
Overall $\bar{x}$	1	6	3	3

[a] Extrapolated from counts provided by Off. Migr. Bird Manage., U.S. Fish and Wildl. Serv., Laurel, Md.

Appendix A, Table 4. Estimated density (pairs/km²) of breeding northern shovelers on study areas ($\bar{x}$ = 26.8 km²) in the Prairie Pothole Region of Canada.

Study area	Density of pairs[a] 1982	1983	1984	1985
Parkland				
Earl Grey				1
Hanley	2	1	<1	4
Hay Lakes		2	3	
Holden		4		
Inchkeith			0	1
Leask			4	3
Moore Park		4	1	
Penhold			<1	1
Yorkton				1
$\bar{x}$	2	3	1	2
Prairie				
Cartwright		<1		
Ceylon		3	1	
Craik			0	1
Denzil			1	2
Gayford				3
Goodwater		7		
Shamrock	5	7	1	1
Tichfield	2			
$\bar{x}$	3	4	1	1
Overall $\bar{x}$	2	3	1	2

[a] Extrapolated from counts provided by Off. Migr. Bird Manage., U.S. Fish and Wildl. Serv., Laurel, Md.

Appendix A, Table 5. Estimated density (pairs/km^2) of breeding northern pintails on study areas ($\bar{x}$ = 26.8 km^2) in the Prairie Pothole Region of Canada.

	Density of pairs[a]			
Study area	1982	1983	1984	1985
Parkland				
Earl Grey				1
Hanley	3	<1	2	1
Hay Lakes		2	1	
Holden		6		
Inchkeith			0	1
Leask			1	<1
Moore Park		2	2	
Penhold			<1	1
Yorkton				1
$\bar{x}$	3	2	1	1
Prairie				
Cartwright		1		
Ceylon		7	2	
Craik			1	2
Denzil			2	4
Gayford				2
Goodwater		7		
Shamrock	5	4	2	2
Tichfield	2			
$\bar{x}$	4	5	2	3
Overall $\bar{x}$	4	4	2	2

[a] Extrapolated from counts provided by Off. Migr. Bird Manage., U.S. Fish and Wildl. Serv., Laurel, Md.

Appendix B. Model employed to estimate habitat preference from observed nest densities. Preference values were derived from least squares mean estimates of habitat effects.

$$Y_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + \gamma_k + \delta_l + \epsilon_{ijkl}$$

where

Y_{ijkl} = $\log([N_{ijkl} + 0.0001]/A_{ijkl})$.
N_{ijkl} = number of nests found on area-year i, half-area-year j within area-year i, habitat k, searched l times.
A_{ijkl} = area searched on area-year i, half-area-year j within area-year i, habitat k, searched l times.
μ = overall mean.
α_i = effect of area-year i.
$\beta_{j(i)}$ = effect of half-area-year j within area-year i.
γ_k = effect of habitat k.
δ_l = effect for number of searches l.

Appendix C. Model employed to describe daily survival rate (DSR) estimates used in estimation of nest success by habitat.

$$Y_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + \gamma_k + \delta_l + \epsilon_{ijkl}$$

where

Y_{ijkl} = observed DSR_{ijkl}.
μ = overall mean.
α_i = effect of area–year i.
$\beta_{j(i)}$ = effect of half-area-year j within area–year i.
γ_k = effect of habitat k.
δ_l = effect for species l.

Appendix D. Species excluded from analysis of daily nest predation rate because nests were not found during each specified search period on study areas in the Prairie Pothole Region of Canada.

		Species excluded				
Study area	Year	Mallard	Gadwall	Blue-winged teal	Northern shoveler	Northern pintail
Cartwright	1983		X		X	
Craik	1984	X	X	X	X	X
Inchkeith	1984	X	X	X		X
Ceylon	1984		X	X		
Shamrock	1985			X		
Hanley	1982		X	X	X	X
	1983					X
	1984				X	
Leask	1984		X			X
	1985					X
Denzil	1984		X			
Holden	1983					X
Hay Lakes	1984		X			X
Penhold	1984		X	X		X
	1985		X	X		X

Appendix E, Table 1. Numbers (n), exposure periods (Days), and estimated rates of success (Rate) of mallard nests by habitat, study area, and year in the Prairie Pothole Region of Canada. Rates of nest success were estimated by the modified Mayfield method (Johnson 1979).

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate
Earl Grey																								
1985	2	27.5	0.27	0			5	49.5	0.24	5	47.0	0.10	1	2.5	0.0	0			3	20.5	<0.01	41	527.2	0.21
Hanley																								
1982	0			0			18	162.0	0.04	0			0			0			4	22.5	<0.01	7	58.5	0.01
1983	0			1	14.5	0.08	16	194.5	0.33	0			0			0			2	12.5	<0.01	6	46.4	0.02
1984	1	20.0	0.17	1	6.5	<0.01	23	189.0	0.03	1	23.0	1.00	0			0			2	7.0	0.0	4	19.5	0.0
1985	0			3	49.0	0.23	9	116.5	0.16	0			0			0			8	96.5	0.07	10	78.5	0.02
Hay Lakes																								
1983	1	5.5	<0.01	7	97.0	0.70	0			34	437.0	0.21	3	29.0	0.08	5	57.0	0.04	0			9	117.5	0.16
1984	2	13.5	<0.01	2	36.5	0.38	0			19	207.7	0.10	2	20.5	0.17	7	87.0	0.19	15	198.0	0.16	18	161.5	0.03
Holden																								
1983	3	6.5	0.0	2	15.0	0.09	18	302.5	0.44	8	121.5	0.31	2	30.0	0.31	0			10	148.5	0.19	5	52.0	0.06
Inchkeith																								
1984	1	2.0	0.0	1	25.0	0.24	0			3	38.0	0.06	0			0			0			0		
1985	0			2	13.5	<0.01	1	1.5	0.0	6	70.0	0.22	0			1	24.0	1.00	7	106.0	0.37	9	109.0	0.14
Leask																								
1984	0			1	10.0	1.00	0			22	184.5	0.10	1	5.0	0.0	1	16.0	1.00	2	9.5	0.0	4	54.5	0.27
1985	0			0			1	2.5	0.0	2	22.5	0.20	1	4.5	0.0	2	17.5	0.01	5	69.5	0.21	16	160.5	0.11
Moore Park																								
1983	5	46.0	0.04	5	73.0	0.38	0			16	129.0	0.02	0			3	31.0	0.03	16	155.1	0.06	12	72.0	0.01
1984	0			6	76.0	0.15	1	3.5	0.0	30	315.5	0.11	0			0			3	8.0	0.0	10	96.0	0.10
Penhold																								
1984	0			0			0			13	136.9	0.12	1	20.0	1.00	0			3	14.0	0.0	10	103.0	0.03
1985	0			0			0			18	225.0	0.20	1	22.0	1.00	0			11	114.0	0.08	9	105.0	0.09
Yorkton																								
1985	0			9	149.5	0.39	3	14.0	0.0	5	49.0	0.11	1	2.5	0.0	6	87.0	0.29	6	118.5	0.41	16	172.0	0.08

Appendix E, Table 1. Continued.

Study area and	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
year	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Cartwright																								
1983	0			7	58.9	0.09	0			3	30.4	0.03	3	20.0	1.00	0			7	89.0	0.09	1	6.5	<0.01
Ceylon																								
1983	2	15.0	<0.01	8	88.0	0.08	187	2,650.0	0.33	3	42.5	0.08	3	27.0	0.07	0			18	124.5	<0.01	16	194.0	0.40
1984	0			3	23.5	0.04	88	817.2	0.05	5	45.5	0.04	0			0			0			0		
Craik																								
1984	0			0			0			3	49.5	0.24	0			0			0			2	15.5	<0.01
1985	0			1	15.5	0.10	1	19.0	1.00	3	38.0	0.15	0			0			0			5	66.5	0.34
Denzil																								
1984	0			2	17.5	0.01	6	35.0	<0.01	8	95.0	0.15	0			0			3	31.0	0.03	3	14.5	0.0
1985	2	3.0	0.0	1	6.5	<0.01	1	1.0	0.0	3	8.0	0.0	2	21.5	0.03	0			4	29.5	0.01	17	157.5	0.04
Gayford																								
1985	0			0			5	45.0	0.02	5	38.0	0.06	0			0			2	47.0	1.00	4	55.5	0.28
Goodwater																								
1983	0			7	54.5	0.03	59	631.0	0.14	2	30.5	0.31	1	4.0	0.0	0			14	102.8	0.01	12	103.0	0.09
Shamrock																								
1982	8	92.5	0.06	2	17.0	0.01	48	825.0	0.46	1	16.0	1.00	6	74.5	0.15	0			8	91.5	0.14	5	94.5	0.47
1983	10	88.5	0.04	7	131.3	0.58	103	1,145.3	0.20	2	17.4	0.01	11	141.5	0.22	0			15	179.0	0.11	9	110.0	0.14
1984	0			4	52.0	0.13	36	314.9	0.03	4	42.5	0.08	2	7.0	0.0	0			9	43.2	0.0	2	8.5	0.0
1985	2	33.5	0.35	8	76.0	0.06	21	225.5	0.06	5	36.0	0.02	1	11.0	0.04	0			4	66.0	1.00	7	92.5	0.10
Tichfield																								
1982	0			3	42.0	1.00	31	397.8	0.14	0			0			0			1	30.0	1.00	4	47.5	0.05

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).

Appendix E, Table 2. Numbers (n), exposure periods (Days), and estimated rates of success (Rate) of gadwall nests by habitat, study area, and year in the Prairie Pothole Region of Canada. Rates of nest success were estimated by the modified Mayfield method (Johnson 1979).

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate
Earl Grey																								
1985	0			0			2	44.0	1.00	1	6.0	<0.01	4	55.5	0.28	0			2	38.0	0.39	4	18.5	<0.01
Hanley																								
1982	0			0			3	65.0	1.00	0			0			0			1	4.0	0.0	1	4.0	0.0
1983	0			1	2.0	1.00	4	19.0	0.0	0			0			0			0			1	4.0	0.0
1984	0			1	5.0	0.0	1	2.0	0.0	0			0			0			0			0		
1985	0			4	63.5	0.57	6	42.0	0.01	0			0			0			3	47.0	0.22	4	37.5	0.02
Hay Lakes																								
1983	0			1	13.0	1.00	0			3	39.0	0.16	0			2	25.0	0.24	0			2	40.0	0.41
1984	0			0			0			1	4.5	0.0	0			2	13.0	<0.01	5	67.5	0.20	2	28.0	0.08
Holden																								
1983	0			2	28.0	0.28	0			0			0			0			0			0		
Inchkeith																								
1984	0			0			0			0			0			0			0			0		
1985	0			0			0			0			0			1	12.0	1.00	3	22.5	0.01	4	26.0	0.01
Leask																								
1984	0			0			0			0			0			1	11.0	1.00	2	9.0	0.0	0		
1985	0			1	18.5	0.14	0			0			3	49.0	0.23	0			0			7	73.5	0.09
Moore Park																								
1983	0			0			0			0			0			0			1	5.0	0.0	3	55.0	0.53
1984	0			0			0			2	14.0	0.08	0			0			0			5	57.0	0.29
Penhold																								
1984	0			0			0			0			0			0			0			0		
1985	0			0			0			3	67.0	1.0	0			0			0			0		
Yorkton																								
1985	0			2	25.0	0.24	1	13.0	0.06	0			0			0			1	18.0	1.00	2	6.0	0.0

Appendix E, Table 2. Continued.

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Cartwright																								
1983	0			0			0			0			1	25.0	1.00	0			1	17.5	0.13	0		
Ceylon																								
1983	0			4	28.5	0.02	106	1,573.5	0.49	0			0			0			3	11.5	0.0	5	57.5	0.08
1984	0			1	17.0	0.12	19	190.5	0.07	0			0			0			2	16.0	0.01	0		
Craik																								
1984	0			0			0			0			0			0			0			0		
1985	0			0			2	30.0	0.31	2	10.5	<0.01	0			0			4	25.5	<0.01	2	10.0	0.0
Denzil																								
1984	0			0			1	6.0	<0.01	2	10.0	0.0	0			0			2	32.0	0.10	2	22.5	0.04
1985	0			0			1	14.0	0.08	0			2	45.0	0.46	0			2	21.5	0.03	4	40.0	0.03
Gayford																								
1985	0			0			5	84.0	0.43	0			1	31.0	1.00	0			4	73.0	0.23	7	136.0	0.35
Goodwater																								
1983	0			3	20.5	<0.01	20	267.5	0.40	0			2	25.5	0.25	0			5	32.5	0.03	7	105.5	0.36
Shamrock																								
1982	0			2	25.5	0.25	24	393.2	0.37	0			5	82.0	0.42	0			4	72.2	0.23	1	14.0	0.08
1983	0			3	47.0	0.47	45	540.0	0.16	0			17	200.0	0.07	0			7	31.5	0.0	6	54.0	0.07
1984	0			0			5	28.0	<0.01	0			1	11.0	0.04	0			0			1	2.5	0.0
1985	0			1	18.0	1.00	2	26.5	0.26	1	4.0	0.0	0			0			3	27.5	0.27	2	32.0	1.00
Tichfield																								
1982	0			1	19.5	0.16	11	234.5	0.47	0			1	5.0	0.0	0			0			1	25.0	0.24

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).

Appendix E, Table 3. Numbers (*n*), exposure periods (Days), and estimated rates of success (Rate) of blue-winged teal nests by habitat, study area, and year in the Prairie Pothole Region of Canada. Rates of nest success were estimated by the modified Mayfield method (Johnson 1979).

Study area and	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
year	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Earl Grey																								
1985	0			1	13.5	0.07	0			5	77.0	0.26	8	123.0	0.33	0			8	94.5	0.05	22	333.4	0.29
Hanley																								
1982	0			1	26.0	1.00	0			0			0			0			2	43.0	0.45	1	11.5	0.05
1983	1	6.4	<0.01	3	55.0	0.54	1	4.0	1.00	1	3.0	0.0	0			0			0			2	6.0	0.0
1984	0			2	20.0	0.03	0			0			0			0			0			0		
1985	0			9	96.5	0.05	1	32.0	1.00	1	12.0	1.00	0			0			5	52.0	0.07	15	184.5	0.18
Hay Lakes																								
1983	0			0			1	4.5	0.0	18	197.0	0.06	11	136.1	0.10	0			3	17.6	<0.01	19	194.0	0.04
1984	0			6	51.5	0.03	1	5.0	<0.01	24	384.0	0.28	5	77.5	0.17	3	39.5	0.17	10	102.0	0.06	20	256.8	0.13
Holden																								
1983	0			12	192.5	0.28	1	28.0	1.00	6	74.0	0.06	0			0			0			1	2.5	0.0
Inchkeith																								
1984	0			0			0			0			0			0			1	29.0	1.00	1	10.0	0.03
1985	0			4	58.5	0.31	1	24.0	1.00	1	10.0	1.00	0			0			3	65.5	0.59	10	113.5	0.08
Leask																								
1984	0			13	186.0	0.27	1	17.5	0.14	9	134.5	0.16	5	63.5	0.11	3	27.5	0.02	4	45.0	0.21	8	115.5	0.22
1985	2	7.0	0.0	14	162.0	0.09	0			7	105.5	0.38	31	386.5	0.11	2	3.0	0.0	11	191.0	0.28	13	88.8	0.01
Moore Park																								
1983	0			6	92.0	0.32	0			11	156.5	0.33	0			3	29.5	0.31	10	114.0	0.12	18	270.5	0.28
1984	0			6	50.0	0.06	0			8	137.0	0.37	0			0			3	19.5	<0.01	33	424.0	0.19
Penhold																								
1984	0			1	16.0	1.00	0			1	6.0	<0.01	2	30.5	0.10	0			0			0		
1985	0			0			0			3	78.0	1.00	0			0			0			0		
Yorkton																								
1985	0			62	768.0	0.14	2	16.0	0.11	3	34.5	0.37	2	19.0	0.02	1	29.0	1.0	7	119.0	0.42	19	173.0	0.05

Appendix E, Table 3. Continued.

Study area and	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
year	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Cartwright																								
1983	0			4	40.0	0.18	0			1	3.5	0.0	1	30.0	1.00	0			4	38.0	0.06	2	37.0	0.39
Ceylon																								
1983	0			33	425.5	0.23	24	326.5	0.31	6	67.5	0.13	2	43.5	0.20	0			7	115.0	0.22	6	83.5	0.12
1984	0			2	17.5	0.02	0			0			0			0			1	26.0	1.00	0		
Craik																								
1984	0			0			0			0			0			0			0			0		
1985	0			2	27.0	0.07	0			1	5.0	<0.01	0			0			7	53.5	0.01	9	67.0	0.01
Denzil																								
1984	0			3	55.5	0.29	0			2	35.0	0.14	0			0			3	30.0	0.10	2	36.0	0.38
1985	0			6	98.5	0.24	0			3	35.0	0.05	3	53.0	0.27	0			9	103.5	0.07	18	179.0	0.05
Gayford																								
1985	0			1	6.0	<0.01	3	61.0	0.57	2	14.0	0.08	2	38.5	0.41	0			4	52.5	0.27	0		
Goodwater																								
1983	0			8	69.0	0.05	7	64.5	0.06	1	24.0	1.00	1	23.0	1.00	0			5	72.0	0.38	4	43.5	0.20
Shamrock																								
1982	0			14	147.2	0.09	1	12.4	0.06	2	39.5	0.42	2	49.0	0.50	0			1	30.0	1.00	2	40.0	1.00
1983	2	5.5	0.0	10	73.7	0.03	3	22.5	0.01	8	93.9	0.11	6	57.5	0.05	0			4	48.7	0.12	6	88.5	0.14
1984	0			0			0			3	31.5	0.33	0			0			1	25.0	1.00	1	3.0	0.0
1985	0			0			0			1	25.0	1.00	0			0			0			0		
Tichfield																								
1982	0			5	46.5	0.05	2	35.5	0.14	0			0			0			3	40.5	0.07	2	25.0	0.06

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).

Appendix E, Table 4. Numbers (*n*), exposure periods (Days), and estimated rates of success (Rate) of northern shoveler nests by habitat, study area, and year in the Prairie Pothole Region of Canada. Rates of nest success were estimated by the modified Mayfield method (Johnson 1979).

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Earl Grey																								
1985	0			0			0			0			2	20.0	0.18	0			2	24.0	0.05	2	10.0	<0.01
Hanley																								
1982	0			2	29.5	0.31	0			3	18.0	<0.01	0			0			0			0		
1983	0			1	4.0	0.0	0			3	61.0	0.57	0			0			0			1	16.0	1.00
1984	0			0			0			0			0			0			0			1	4.0	0.0
1985	0			4	67.0	0.36	2	24.0	0.24	2	39.5	0.42	0			0			7	58.0	0.02	8	70.0	0.03
Hay Lakes																								
1983	0			1	10.0	1.00	0			8	64.5	0.02	5	37.5	0.02	0			4	48.0	0.24	8	104.4	0.09
1984	0			0			0			16	232.0	0.26	0			0			2	15.5	0.10	6	47.5	0.02
Holden																								
1983	0			14	158.0	0.11	2	15.5	0.10	10	138.0	0.13	1	33.0	1.00	0			0			5	25.0	<0.01
Inchkeith																								
1984	0			2	39.5	0.42	1	9.5	0.02	0			0			0			0			1	1.5	0.0
1985	1	2.0	0.0	3	25.0	0.01	0			0			0			0			2	16.0	0.11	7	51.5	0.03
Leask																								
1984	0			3	30.0	0.10	0			11	133.0	0.21	2	9.5	0.02	0			2	14.5	0.01	3	21.0	0.03
1985	0			5	18.0	0.0	0			2	20.5	0.18	7	80.5	0.07	0			1	5.0	<0.01	6	73.0	0.15
Moore Park																								
1983	0			1	2.5	0.0	0			5	89.0	0.68	0			0			2	19.0	0.02	5	26.0	<0.01
1984	0			1	6.0	<0.01	0			3	15.0	<0.01	0			0			1	4.0	0.0	11	143.0	0.14
Penhold																								
1984	0			1	7.5	0.01	0			1	5.5	<0.01	2	7.5	0.0	0			1	7.0	0.01	0		
1985	0			1	22.0	1.00	0			2	37.5	0.40	0			0			1	5.5	<0.01	0		
Yorkton																								
1985	0			8	88.0	0.14	1	3.0	0.0	2	29.5	0.31	0			0			1	22.0	1.00	4	40.0	0.03

Appendix E, Table 4. Continued.

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Cartwright																								
1983	0			1	4.0	0.0	0			0			0			0			1	31.0	1.0	0		
Ceylon																								
1983	0			25	314.0	0.30	13	175.0	0.25	4	70.0	0.23	0			0			5	39.5	0.01	5	71.5	0.14
1984	0			2	13.5	0.07	1	11.0	0.04	1	3.0	0.0	0			0			0			0		
Craik																								
1984	0			0			0			0			0			0			0			0		
1985	0			1	20.0	1.00	0			1	4.5	0.0	0			0			3	15.0	<0.01	3	31.5	0.03
Denzil																								
1984	0			5	43.0	0.04	0			2	16.0	0.01	0			0			2	16.5	0.01	1	14.5	0.09
1985	0			5	72.5	0.39	0			3	24.0	0.05	5	55.0	0.08	0			7	56.5	0.01	8	72.0	0.05
Gayford																								
1985	0			3	53.0	0.52	0			0			0			0			1	16.0	1.00	0		
Goodwater																								
1983	0			10	171.5	0.55	4	52.5	0.52	3	38.5	0.16	2	29.5	0.31	0			7	85.5	0.13	2	32.0	0.34
Shamrock																								
1982	1	11.5	0.05	22	308.9	0.23	4	50.0	0.25	2	15.0	0.01	14	170.0	0.24	0			12	130.5	0.07	1	8.0	1.00
1983	6	55.5	0.04	18	152.0	0.13	10	136.5	0.28	2	11.5	<0.01	17	252.0	0.22	0			8	101.0	0.18	8	100.9	0.12
1984	0			2	8.5	0.0	0			0			0			0			0			0		
1985	0			0			0			0			1	20.0	1.00	0			1	3.5	0.0	3	37.0	0.15
Tichfield																								
1982	0			2	23.0	0.22	2	12.5	<0.01	0			1	20.0	1.00	0			4	23.0	<0.01	2	49.0	1.00

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).

Appendix E, Table 5. Numbers (n), exposure periods (Days), and estimated rates of success (Rate) of northern pintail nests by habitat, study area, and year in the Prairie Pothole Region of Canada. Rates of nest success were estimated by the modified Mayfield method (Johnson 1979).

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate	n	Days	Rate
Earl Grey																								
1985	3	17.5	<0.01	0			0			2	6.5	0.01	4	37.5	0.03	0			1	3.5	0.0	6	77.0	0.28
Hanley																								
1982	1	6.5	0.01	3	19.0	<0.01	1	2.0	0.0	1	18.0	0.16	0			0			1	4.0	0.0	0		
1983	1	6.4	<0.01	0			3	38.5	0.43	0			0			0			3	9.0	0.0	1	3.0	0.0
1984	2	20.5	0.04	1	9.0	0.02	4	61.0	0.34	2	6.0	0.0	0			0			1	7.0	0.01	2	5.5	0.0
1985	0			3	22.0	0.01	6	44.5	0.02	0			0			0			5	54.0	0.16	6	58.0	0.33
Hay Lakes																								
1983	1	10.5	0.04	1	2.5	0.0	0			8	98.5	0.27	1	12.0	1.00	0			0			2	19.0	0.18
1984	0			0			0			4	36.0	0.06	2	6.0	0.0	0			2	12.5	0.07	2	20.5	0.04
Holden																								
1983	20	42.0	0.0	6	60.5	0.06	2	33.5	0.38	1	16.5	0.14	1	8.0	1.00	0			6	85.0	0.21	6	60.0	0.06
Inchkeith																								
1984	1	2.5	0.0	1	10.5	0.04	0			0			0			0			0			0		
1985	1	2.0	0.0	2	35.0	0.15	1	16.5	0.14	1	10.0	1.00	0			0			2	5.0	0.0	4	41.5	0.09
Leask																								
1984	0			0			0			2	20.0	1.00	0			0			1	16.0	0.13	1	10.0	1.00
1985	0			0			0			0			1	20.0	1.00	0			1	5.5	<0.01	0		
Moore Park																								
1983	0			3	17.0	<0.01	0			4	24.5	<0.01	0			1	22.0	1.00	3	29.0	0.10	4	18.5	<0.01
1984	0			2	11.5	<0.01	0			8	55.5	0.03	0			0			1	5.0	<0.01	5	44.0	0.05
Penhold																								
1984	0			0			0			0			0			0			0			0		
1985	0			0			0			9	140.5	0.50	0			0			0			0		
Yorkton																								
1985	2	12.0	<0.01	3	43.5	0.48	0			0			0			0			2	8.0	0.0	2	2.5	0.0

Appendix E, Table 5. Continued.

Study area and year	Cropland			Grass			Brush			Wetland			Hayland			Woodland			Right-of-way			Odd area[a]		
	n	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate	*n*	Days	Rate
Cartwright																								
1983	0			4	34.0	0.02	0			1	25.0	1.00	0			0			3	35.0	0.06	0		
Ceylon																								
1983	2	25.5	0.28	9	87.0	0.05	68	759.5	0.34	1	6.5	0.01	5	54.0	0.55	0			4	43.5	0.10	4	43.0	0.10
1984	0			2	38.5	0.43	25	202.9	0.06	3	20.5	0.04	0			0			2	11.5	<0.01	0		
Craik																								
1984	0			0			0			0			0			0			0			0		
1985	4	51.0	0.14	0			0			0			0			0			1	14.5	0.10	4	40.0	0.08
Denzil																								
1984	2	5.0	0.0	2	26.5	0.08	0			1	5.0	<0.01	0			0			0			2	15.0	0.01
1985	14	140.0	0.12	3	24.5	0.26	6	32.0	<0.01	0			10	92.0	0.05	0			5	36.4	0.02	9	68.0	0.01
Gayford																								
1985	0			0			6	69.0	0.15	3	17.5	<0.01	2	21.5	0.04	0			1	4.0	1.00	1	2.5	0.0
Goodwater																								
1983	6	36.5	<0.01	11	134.0	0.18	50	426.0	0.17	0			2	13.5	0.09	0			8	74.5	0.07	2	17.5	0.02
Shamrock																								
1982	19	159.5	0.07	7	95.4	0.25	40	487.6	0.26	0			15	241.0	0.51	0			5	71.5	0.40	0		
1983	6	63.5	0.07	6	74.5	0.17	51	580.9	0.31	0			10	64.5	0.01	0			5	68.5	0.39	3	46.5	0.25
1984	4	16.5	0.0	2	8.5	0.02	8	64.5	0.04	2	5.0	0.0	3	33.5	0.38	0			1	11.5	0.05	0		
1985	3	10.5	0.0	1	20.0	1.0	9	76.0	0.05	3	32.0	0.13	2	26.0	0.29	0			1	4.0	0.0	2	7.0	0.0
Tichfield																								
1982	1	5.0	<0.01	3	59.0	0.19	11	185.5	0.35	0			0			0			0			1	3.0	0.0

[a] Odd area included patches of cover <2 ha in size and an array of features usually found in Cropland (e.g., rock piles, gravel borrow pits, narrow borders of upland vegetation around Wetland and along fences between areas of Cropland).