Northern pintail nest site selection, nest success, renesting ecology and survival in the intensively farmed prairies of southern Saskatchewan: an evaluation of the ecological trap hypothesis

Kenneth Daniel Richkus

Louisiana State University and Agricultural and Mechanical College

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NORTHERN PINTAIL NEST SITE SELECTION, NEST SUCCESS, RENESTING ECOLOGY, AND SURVIVAL IN THE INTENSIVELY FARMED PRAIRIES OF SOUTHERN SASKATCHEWAN: AN EVALUATION OF THE ECOLOGICAL TRAP HYPOTHESIS

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College
In partial fulfillment of the Requirements for the degree of Doctor of Philosophy

in

The School of Forestry, Wildlife, and Fisheries

by
Kenneth Daniel Richkus
B.S., Virginia Polytechnic Institute and State University, 1996
May 2002
DEDICATION

This work is dedicated to my grandfather,

Edmund Ward.

It was through our relationship that I learned to respect and see the beauty in the natural world. The times we spent together hunting and fishing were some of the best of my life and changed the course of my life forever.
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I am indebted to many people who contributed to this project and to whom I owe my thanks. It has been a great honor to work with Dr. Frank Rohwer, my major professor. I have grown tremendously as a scientist and an educator through my professional and personal relationship with him. Frank offered unending support, provided motivation when I needed to be pushed, yet gave me great freedom throughout my entire study for which I am grateful. I only hope I can uphold his commitment to science in my future endeavors.

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ABSTRACT

Unlike most prairie nesting ducks (Anas spp.), the North American population of northern pintails (A. acuta, hereafter pintails) has failed to respond as expected to improved wetland conditions on the U.S. and Canadian prairies during the mid to late 1990s. My primary objectives were to test the “ecological trap hypothesis” on a landscape level by examining pintail nest site selection and nest success in a highly agricultural environment in southern Saskatchewan. I also used radiotelemetry to estimate renesting and breeding season survival rates of female pintails; two parameters that are important in productivity and life cycle models. Most (51%) pintail nests were found in crop stubble and generally pintails nested in habitats in proportion to their availability on the landscape. In contrast, most (82%) mallard nests were located in edge and grassland habitats. Mallards nested in habitats with dense cover in greater proportion to their availability and avoided crop stubble. Nest success estimates in crop stubble were lower (<1-4% vs. 6-37%) than the surrounding habitats with greater cover. Nest success estimates in crop stubble were abysmal largely due to high rates of nest predation. Only 20-33% of nests in crop stubble failed due to spring cultivation. For 1998, 1999, and 2000, overall renesting rates for females trapped throughout the nesting season were 50%, 71%, and 41%, but were 61%, 90% and 62% when only first nesting females were included. Renesting propensity declined seasonally, but at different rates among years likely due to variation in wetland abundance. Most (58%) females renested, but few (37%) initiated multiple renests. Survival rate for my 75-day interval (April 30 – 14 July) was 0.81 ± 0.05. Cause-specific mortality rates were greater for avian predators (0.14 ± 0.04) than other sources of mortality. The pintail’s high propensity to nest in crop stubble where nest success is low coupled with lower renesting and breeding season survival rates than mallards
may partially explain their meager response to improved wetland conditions. Management programs to facilitate pintail recovery should be targeted at increasing nest success by providing safe nesting habitat.
CHAPTER 1. INTRODUCTION

Since the implementation of the U. S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) May Breeding Population and Habitat Survey in 1955, continental population of northern pintail (Anas acuta; hereafter – pintail) have historically been highly correlated with May ponds in the Prairie Pothole Region (PPR). The drought of the 1980’s and early 1990’s resulted in dramatic declines in pond numbers and most prairie nesting dabbling ducks, including pintails. However, for most ducks, successive wet years in the mid to late 1990s have resulted in population improvements to levels that exceeded objectives set by the North American Waterfowl Management Plan (NAWMP). For example, mallards (A. platyrhynchos), the indicator species for the NAWMP, have rebounded from 4.9 million breeding individuals in 1985, to a near record high of 11.1 million individuals in 1999 (USFWS 2000, Fig. 1.1). Similarly, blue-winged teal (A. discors) recovered from a record low of 2.8 million in 1990, to a record high of 7.2 million in 1999 (USFWS 2000).

Unfortunately, the breeding population (BPOP) of pintails has failed to respond as expected to increasing pond numbers on the prairies and has shown only a modest recovery from the record low of 1.8 million in 1991 (USFWS 2000). In 1999, the pintail BPOP of 3.1 million was 30% below their long-term average (Fig. 1.1) and they were the only dabbling duck below NAWMP goals (USFWS 2000). Considering the large BPOP estimates attained during previous periods of abundant May ponds, the current response by pintails to improved wetland conditions is perplexing, but can be attributed to poor survival, poor recruitment, or some combination of these 2 parameters.

The pintail population decline through the 1980’s probably provided the impetus for much of the recent research on pintails. Dry conditions on the prairie breeding grounds
Figure 1.1. Breeding population (BPOP) estimates for northern pintails and mallards for the traditional survey area (strata 1-18, 20-50, 75-77).
during the 1980s were a likely cause for the decline (USFWS 1990), but Raveling and Heitmeyer (1989) suggested that habitat conditions on the wintering grounds can have a large impact on pintail population processes, especially when spring seasons were dry. Subsequently, there were several studies to assess winter survival of female pintails. Miller et al. (1995) estimated winter survival to be 0.87 in Sacramento Valley, California, the state that supports the largest wintering population of pintails (Bellrose 1980). In Sinaloa, Mexico, the winter survival estimate of 0.91 was similarly high (Migoya and Baldassarre 1995). These reasonably high, telemetry-based estimates of winter survival indicate that the pintail decline and meager recovery does not appear to be related to winter habitat conditions, which affect female survival. However, both of these studies reported that harvest was the major source of winter mortality. In southwestern Louisiana, Cox et al. (1998) estimated winter survival to be only 0.55 and 0.71 for immatures and adults, with hunting as the major source of winter mortality for both age classes (0.29 and 0.13). These relatively low estimates of winter survival and high harvest rates in Louisiana indicate that female survival during the winter is variable and might limit population growth.

Hestbeck (1993) indicated that the pintail population recovery in the late 1970’s might have been related to a concomitant increase in female survival due to restrictive harvest regulations. In an attempt to increase winter survival, restrictive harvest regulations were implemented between 1988-1991, compared to the liberal regulations between 1976-1984, where limits on pintails could reach 10 per day. These restrictive regulations led to a 50% reduction in direct band recovery rates for females in the 3 eastern flyways (Johnson and Moore 1996). Furthermore, in the last decade band recovery rates of adult pintails have been < 2% of Pacific Flyway preseason bandings (Dubovsky 1996) and < 4% of winter bandings
Despite conservative harvest regulations and diminutive band recovery rates, which may be the best index of harvest rates, the pintail population has shown little improvement for most of the 1990’s. Overall, there is little evidence to support the hypothesis that poor winter survival and high harvest rates are responsible for decline and meager growth of the pintail population.

Hestbeck (1995) suggested that the pintail decline and slow recovery may reflect poor recruitment rather than inadequate winter survival. Juvenile to adult age ratios in the harvest, which may be our best index of recruitment, have typically been lower for pintails than other dabbling ducks (Padding et al. 1998). Hestbeck (1995, 1996) also noted that pintail age ratios in the Pacific Flyway were generally lower in recent wet years on the prairies than during the wet conditions on the prairies in the late 1960s. Although pintail age ratios in the harvest have been variable, this negative trend suggests that pintail reproductive success during the last decade may have been problematic (Hestbeck 1996).

Similarly, Miller and Duncan (1999) reviewed several potential explanations for poor pintail status and concluded that declining reproductive success was probably the greatest impediment to pintail population growth. They suggested that a shift away from fall tillage, which leaves crop stubble on the prairies over the winter, has created an “ecological trap” for nesting females. The ecological trap hypothesis suggests that pintail females are attracted to the abundant crop stubble for nesting and subsequently suffer high rates of nest failure due to spring cultivation. In Chapter 1, I tested Miller and Duncan’s (1999) “ecological trap hypothesis” on a landscape level by examining pintail nest site selection and nest success in a highly agricultural environment. I predicted that a large fraction of pintails would nest in crop stubble and subsequently have their nests destroyed by farm machinery during spring.
cultivation; therefore in Chapter 2, I examined pintail renesting ecology. Renesting, the laying of a replacement clutch following failure of a previous nesting attempt (Sowls 1955), is a common reproductive strategy that allows female ducks to compensate for high nest failure rates and increase their seasonal reproductive success (Cowardin and Johnson 1979). Because renesting is an important component of hen success, knowledge of pintail renesting rates and factors that affect renesting propensity are important to accurately model productivity (Carlson et al. 1993), and develop reliable life-cycle models (Flint et al. 1998).

Annual survival rates derived from banding data also are crucial for productivity and population modeling (Carlson et al. 1993, Flint et al. 1998); however, these estimates do not allow survival to be partitioned into segments of the annual cycle or identify cause-specific sources of natural mortality. Partitioned survival estimates are crucial to improve our understanding of waterfowl population regulation, develop accurate population models, and improve management decisions (Johnson et al. 1992). Several studies have estimated survival of female pintails on key wintering areas, but data on breeding season survival are lacking. In Chapter 3, I estimated survival and mortality patterns of female pintails during the nesting season. Females often suffer greater mortality during the breeding season than during other segments of the annual cycle due to increased vulnerability to mammalian and avian predation (Johnson et al. 1992).

Interspecific comparisons of reproductive or survival parameters are important for developing or testing hypotheses regarding evolutionary life history strategies and developing species-specific management programs (Johnson et al. 1992). However, many researchers that make interspecific comparisons often fail to account for spatial and temporal variation among studies. I believe that inferences generated from such comparisons should be made
with caution because environmental conditions such as climate, wetland abundance, food availability and predation pressures may vary spatially and temporally. Throughout my study, I treated mallards as a control relative to pintails. Mallards are a species with a similar early nest initiation date as pintails (Greenwood et al. 1995), are common in prairie Saskatchewan (Bellrose 1980), and in contrast to pintails, have increased dramatically during the mid to late 1990s (USFWS 2000). In Chapters 4 and 5, I examined renesting ecology and survival and mortality patterns of pintails and mallards within the same landscape and during the same year in an attempt to identify differences in their breeding ecology that might explain the persistently low pintail BPOPs and meager response to improved wetland conditions.

**LITERATURE CITED**


CHAPTER 2. NORTHERN PINTAIL NEST SITE SELECTION AND NEST SUCCESS

For most prairie nesting dabbling ducks (*Anas* spp.), successive wet years on the prairies during the mid to late 1990s have resulted in population improvements to levels that exceeded the objectives set by the Northern American Waterfowl Management Plan (NAWMP; United States Fish and Wildlife Service [USFWS] 2000). For example, mallards (*A. platyrhynchos*) rebounded from 4.9 million breeding individuals in 1985, to a near record high of 10.8 million in 1999 (USFWS 2000). Unfortunately, the continental population of northern pintails (*A. acuta*; hereafter pintails) has failed to respond as expected to improved wetland habitat conditions on the prairies and has shown only a modest recovery from the record low of 1.8 million in 1991 (USFWS 2000). In 1999, the pintail breeding population (BPOP) of 3.1 million was 30% below the long-term average and pintails were the only species of dabbling duck below NAWMP population goals (USFWS 2000).

Persistently low pintail population levels and a meager response to improved wetland conditions can be attributed to poor survival, poor recruitment, or some combination of these 2 key parameters. Miller and Duncan (1999) reviewed several potential explanations for poor pintail status for these 2 parameters and concluded that declining reproductive success was probably the greatest impediment to pintail population growth. They suggested that a shift away from fall tillage on the prairie breeding areas has created an “ecological trap” for nesting females. The ecological trap hypothesis suggests that pintail females are attracted to the abundant crop stubble for nesting and subsequently suffer high rates of nest failure due to spring cultivation.

The basis of this ecological trap hypothesis is that habitat in the prairies has changed over the past decade. Conservation tillage practices, such as the elimination of fall tillage and
no-till farming have increased dramatically in the last decade (Statistics Canada 1997) especially in Saskatchewan, a province in the prairie pothole region of particular importance to nesting pintails (Bethke and Nudds 1995, Smith 1995, Miller and Duncan 1999). Such tillage practices leave crop stubble on fields after harvest and have resulted in an increased availability of crop stubble habitat in the Canadian prairies. The area of no-till land in Canada increased 135% between 1991 and 1996 to 4.6 million ha, 64% of which are in Saskatchewan (Statistics Canada 1997).

Bethke and Nudds (1995) estimated that the pintail BPOP in 1989 was only 45% of the predicted abundance based on the historical relationship between pintail BPOPs and wetland conditions during 1955-74. USFWS survey strata 32 in prairie Saskatchewan accounted for the greatest proportion (27%) of this deficit of 1.2 million pintails. Bethke and Nudds (1995) attributed this deficit to the westward expansion of small grain agriculture and intensified land use in the Canadian prairies. Hence, there is strong anecdotal evidence to support the hypothesis that, on a large geographic scale (USFWS survey strata), agricultural land use and perhaps tillage practices may have negative impacts on pintail BPOPs.

My primary objectives were to test Miller and Duncan’s (1999) “ecological trap hypothesis” on a landscape level by examining pintail nest site selection and nest success in a highly agricultural environment in the core of the pintail’s prairie breeding range. I predicted that pintails would nest in crop stubble habitats at a greater frequency than mallards, and pintails would nest in habitats in proportion to their availability on the landscape, while mallards will likely “avoid” crop stubble habitats. I also predicted productivity (nest success) would be lower in crop stubble than surrounding grassland habitats due to catastrophic losses to farm machinery during spring cultivation.
I suspected pintails were more likely to be caught in the ecological trap for several reasons. First, pintails have a higher propensity to nest in sparse cover, including cropland, relative to other ducks (Milonski 1958, Keith 1961, Stoudt 1971, Higgins 1977, Klett et al. 1988, Greenwood et al. 1995). Second, pintails initiate nests early in the breeding season (Bellrose 1980, Duncan 1987b, Greenwood, 1995, Guyn and Clark 2000) when crop stubble is most available. Later nesters like blue-winged teal (A. discors) and gadwall (A. strepera), have little opportunity to nest in crop stubble because the chronology of seeding for cereal grains and oil-seed crops is ahead of their nesting chronology. Finally, pintails will nest substantial distances from water relative to other ducks (Keith 1961, Bellrose 1980, Duncan 1987b). These 3 aspects of the pintail’s nesting ecology may make them more vulnerable to the ecological trap than other sympatric nesting ducks.

I treated mallards as a control relative to pintails in an attempt to identify differences in their breeding ecology that might explain the persistently low pintail BPOPs and poor response to improved wetland conditions. Mallards are a species with an early nest initiation date similar to pintails (Greenwood et al. 1995), are common in prairie Saskatchewan, and in contrast to pintails, have increased dramatically during the mid to late 1990s (USFWS 2000). In addition to examining nest site selection and nest success, I tested for differences in visual concealment of nests, distance to nearest water, and clutch size between pintails and mallards.

**STUDY AREA**

I conducted research from April to July during 1998-2000 on a 16,576 ha (64 square-mile) block on the edge of the Missouri Coteau in south-central Saskatchewan (49°35’ N, 104°29’ W), centered about 10 km south and 40 km west of the town of Weyburn, SK. Topography ranged from gently rolling pastures in the southwest to relatively flat cropland in
the northeast. Wetlands interspersed in these habitats ranged from small ephemeral basins (<1 ha) to a large (approx 290 ha) semi-permanent basin. Approximately 13,095 ha (79%) were dominated by cereal grain and oil-seed agriculture, primarily spring wheat (*Triticum spp.*) and canola (*Brassica spp.*). During my study, 81-89% of the cropland was left over the winter in crop stubble; the remaining cropland was tilled in the fall, leaving bare dirt. Other lands in the study area were pastures, hayfields, pond margins, road right-of-ways, odd areas (small areas of grass ≤ 2 ha found in cropland such as rock piles and fence rows), and 256 ha of nesting cover planted under the NAWMP (USFWS et al. 1994). Wetland densities were 27% and 30% below the long-term average for this region in 1998 and 2000, and 26% above the long-term average in 1999 (USFWS 2000). This study site was selected because of consistently high pintail breeding pair densities determined from the Canadian Wildlife Service (CWS) May counts (USFWS 2000), and the large proportion of the cropland that was left over winter in stubble. I believe that this study site is typical of much of the pintail’s prairie breeding range. Based on observations and track surveys (Sargeant et al. 1993, Sovada et al. 1995) potential predators of upland nesting waterfowl that were abundant included red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and coyote (*Canis latrans*); American badger (*Taxidea taxus*), Franklin’s ground squirrel (*Spermophilus franklinii*), American crow (*Corvus brachyryhnchos*), and black-billed magpie (*Pica pica*) were less common.

**METHODS**

**Field Procedures**

Habitat Classification. -- I used ARC/INFO digitizing software (ESRI 1994) to determine habitat composition, area of each habitat class in each quarter-section (64.8 ha [160
block) from aerial photographs taken in early April 1998. Area of each habitat class in 1999 and 2000 were extrapolated from 1998 photographs after ground truthing each block. I initially classified habitats as: 1) fall-tilled cropland (bare dirt), 2) crop stubble, 3) pasture lands 4) hayfields (usually a 50/50 mixture of alfalfa [Medicago sativa] and crested wheat grass [Agropyron cristatum]), 5) NAWMP cover 6) right-of-way, 7) wetland margins, and 8) odd areas. Due to sample size restrictions, I pooled some habitats based on similar vegetative structure and polygon size and shape. Pasture lands, hayfields, and NAWMP cover were pooled together and referred to as grassland habitats. I pooled right-of-way, wetland margins, and odd areas and referred to this grouping as edge habitats. Because my study area is greatly impacted by agriculture, I drove the study area every 5-7 days to record cultivation dates and changes in habitat classification.

Nest Searching and Nest Visits. -- I searched all upland habitats in blocks starting in late April and ceasing in late June in 1998 and early July in 1999 and 2000. Searching was conducted between 0800 and 1400 hrs when females were most likely to be present on incubation and laying stage nests (Gloutney et al. 1993). Waterfowl nests in grassland cover were located by systematically dragging a 70 m chain between two ATVs (Higgins 1977, Klett et al. 1986). Due to lower nest densities in crop stubble, sparser residual vegetation, and the large proportion of crop stubble on the study area, a 200 m cable was used to search cropland. Where chain or cable drags could not be used, I walked and beat vegetation with sticks to flush nesting females (Greenwood et al. 1995). I marked nests with a 50 cm willow (Salix spp.) stick placed 1 m south and an individually numbered, 90 cm white lathe 20 m north of each nest. I recorded species, habitat type, clutch size, and developmental stage (Weller 1956) for each nest and revisited each nest at 7-8 day intervals to determine fate (Klett
et al. 1986). Nests were classified as successful if ≥ 1 egg hatched determined by the presence of eggshell membranes or ducklings in the nest bowl (Sovada et al. 1995), abandoned due to investigator, weather, or unknown, and destroyed due to predation, farm machinery, or investigator activity.

On the second visit to each nest, I verified species identity, recorded number of eggs, and completed clutch size. I used a Robel pole marked with 5 cm increments to index visual obstruction (VOR) of each nest (Robel et al. 1970). The Robel pole was placed vertically at the north side of the nest bowl and observed from 5 m south of each nest at a height of approximately 1 meter. Distance to nearest water (DISTWET) was measured with a distance tape if ≤ 200 m or Global Positioning System if > 200 m. All procedures in this study were approved by Louisiana State University Institutional Animal Care and Use Protocol (A98-3), and University of Saskatchewan on behalf on the Canadian Council of Animal Care (03622-AI).

**Statistical Analysis**

Nest Site Selection. -- I conducted all analysis using SAS statistical software (SAS Institute Inc. 1999) unless otherwise noted. In 1998, I concentrated my nest searches in areas known to contain high densities of pintail nests to ensure adequate samples of radiomarked females for concurrent studies of brood survival (Peterson 1999) and induced renesting (Chapter 2, 4). This non-random search protocol biased my estimates of habitat use and availability; therefore, I did not calculate estimates of nesting habitat preference for females in 1998 and only reported number of nests found in each habitat type. In 1999 and 2000, I randomly selected blocks for searching and searched all upland habitats within each block. However, crop stubble was not searched when precipitation made conditions unfavorable for
searching or once it was cultivated or contained standing crop. Blocks for searching were sampled with replacement, but not less than 21 days between searches. The only deviation from this random sampling protocol occurred on 9 of 256 blocks each year. I failed to secure landowner permission on 4 blocks within the study area that were primarily crop stubble, 4 blocks of pasturelands were not searched when livestock were present, and 1 block was never searched because it contained the small town of Khedive, SK where there were multiple private residences and buildings.

For habitat use and availability analyses, I defined available nesting habitat as the area of each habitat type that was searched. Although the availability of crop stubble on the study area changed throughout the nesting season due to tillage, by defining available habitat as the area searched, this change is reflected in my estimate of habitat availability. Because I searched blocks randomly, I assumed that on any given date, the probability that a habitat was searched was equal to the proportion of that habitat on the study area on that date with the exception of cropland that was tilled (spring or previous fall) or contained standing crop. Similar to Greenwood et al. (1995), I believe that tilled habitats were unsuitable nesting habitat for pintails or mallards. During 1998-2000, I searched 1066 ha of fall-tilled habitat and found 1 pintail and no mallard nests. Furthermore, I believe that standing crop from spring seeding, which does not emerge until approximately early to mid June is largely unavailable for early nesting species like pintails and mallards. In a concurrent study of induced renesting, only 1 of 91 nest initiations of radiomarked pintails and 2 of 45 radiomarked mallard nest initiations were in standing crop (Richkus and Rohwer, unpublished data). Therefore, I excluded cropland habitats that were tilled or contained standing crop from analyses of habitat use and availability and limited my inferences on habitat use to
suitable and available nesting habitats for each species. In this analysis, I included only nests found while actively searching with chain or cable drags or beat outs.

I used a chi square goodness-of-fit test (PROC GENMOD) to analyze nesting habitat use and availability for pintails and mallards in 1999 and 2000 (Neu et al. 1974). When the test statistic indicated a difference between nesting habitat use and availability, I calculated 95% Bonferroni simultaneous confidence intervals to determine habitat preference (Byers et al. 1984, Thomas and Taylor 1990). A fundamental assumption of the Neu et al. (1974) method is that a relationship exists between density and relative preference and this assumption is violated if detectability varies among habitat types (Thomas and Taylor 1990). Similar to Greenwood et al. (1995), I believe that it was reasonable to assume that my nest searching methods were equally effective in each habitat type. However, my estimates of daily survival rates (DSRs) of nests varied greatly among habitat types (see below), potentially biasing my nest density estimates. Apparent nest densities are an underestimate of the true nest densities because not all initiated nests are found (Miller and Johnson 1978). Some initiated nests go undetected because they are destroyed before they can be located by researchers (Miller and Johnson 1978). In my study, the negative bias in apparent nest densities is not equal among habitat types because DSRs differed among habitat types, which violates a major assumption of the Neu et al. (1974) method. To account for this unequal bias, I estimated the number of nest initiations (adjusted nest numbers) in each habitat type -year combination where the adjusted nest number = n/DSR^a, and n = number of nests found in a habitat, DSR = daily survival rate for that habitat, and a = mean age of nests when found in the habitat (Cowardin et al. 1985). When I adjusted the apparent nest numbers in crop
stubble, I calculated DSRs excluding nests destroyed by spring cultivation because I did not search crop stubble habitats after they were cultivated.

Nest Site Characteristics, Clutch Size, and Nesting Chronology. -- I used 3-way analysis of variance (ANOVA, PROC GLM) in a completely randomized design to test effects of species (pintail, mallard), habitat type (crop stubble, edge habitats, grassland habitats), and year (1998, 1999, 2000) and their interactions on VOR and DISTWET. I used Least Squares Means (LSMEANS) with a Tukey-Kramer adjustment for multiple comparisons to compare means of significant effects. Analyses of nest site characteristics included nests found incidentally and while actively searching. I used an analysis of covariance (ANCOVA) to test for variation in clutch size in relation to species (pintail, mallard), year (1998, 1999, 2000), and nest initiation date. Nests were excluded from clutch size analysis if they were depredated before a full clutch was laid (no eggs added in 2 days), or showed evidence of a partial depredation or nest parasitism. I used PROC UNIVARIATE to obtain summary statistics for the median date and interquartile ranges of nest initiation and cultivation. I used an analysis of variance (ANOVA, PROC GLM) to determine if median nest initiation and cultivation dates and interquartile ranges differed between species. I used the interquartile range (the difference between the third and first quartiles) as a measure of central span of the nesting period (Greenwood et al. 1995).

Nest Success. -- I used the Mayfield method (Mayfield 1961, 1975) as modified by Johnson (1979) to calculate DSRs and standard errors of nests in each year-habitat combination. I included nests found incidentally and while actively searching in my calculations of nest success. Nests that were abandoned or damaged due to investigator activity, or had no determination of fate were excluded from calculations (Greenwood et al.
I also excluded pintail and mallard nests if females were nest trapped and radiomarked for concurrent studies of induced renesting (Chapter 2, 4) and female survival (Chapter 3, 5), and pintail nests that were fenced in 1998 to reduce the risk of predation for a concurrent brood survival study (Peterson 1999). I had inadequate sample sizes (≤ 3 nests) and exposure days in some year-habitat combinations to calculate meaningful DSRs and standard errors for pintails separately. Therefore, I calculated DSRs for all dabbling ducks combined to obtain sound estimates of DSR in each habitat type. Species differences in nest success within habitats are seldom statistically significant (Klett et al. 1988, Greenwood et al. 1995). I simultaneously tested for variation in DSRs for all species combined relative to year (1998, 1999, 2000), and habitat type (crop stubble, edge habitats, and grassland habitats) using a generalized chi-square hypothesis testing procedure outlined by Sauer and Williams (1989) in program CONTRAST (Hines and Sauer 1989). To simplify interpretation, DSRs were converted to nest success estimates (P) where P = 100*(DSR)\(^I\) and I = 32 for pintails, the sum of the average laying duration plus the incubation interval in days (Klett et al. 1986). All means are reported ± standard error unless otherwise noted.

**RESULTS**

**Habitat Preference**

I found 1340 duck nests while actively searching during 1998-2000. Mallards (33%) and pintails (24%) were the dominant species found, with blue-winged teal (17%), gadwall (15%), northern shoveler (A. clypeata, 9%), and other dabbling ducks (2%) making up the remainder. Fifty-one percent of the pintail nests I found were located in crop stubble compared to only 18% of mallard nests (Table 2.1.). Pintails nested in habitats in proportion to their availability in 1999 ($\chi^2_2 = 0.72, P = 0.70$, Fig. 2.1), but in 2000, pintails used crop
Table 2.1. Number (%) of northern pintail nests found in each habitat type and hectares of each habitat type searched (%) in southern Saskatchewan, 1998-2000.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Year</th>
<th>Pintail</th>
<th>Mallard</th>
<th>Year</th>
<th>Pintail</th>
<th>Mallard</th>
<th>Year</th>
<th>Pintail</th>
<th>Mallard</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop Stubble</td>
<td>1998</td>
<td>41 (37)</td>
<td>27 (16)</td>
<td>1999</td>
<td>5145 (67)</td>
<td>87 (67)</td>
<td>2000</td>
<td>3255 (56)</td>
<td>32 (42)</td>
</tr>
<tr>
<td>Edge Habitats(^a)</td>
<td>1998</td>
<td>11 (10)</td>
<td>72 (42)</td>
<td>1999</td>
<td>425 (6)</td>
<td>5 (4)</td>
<td>2000</td>
<td>286 (5)</td>
<td>4 (5)</td>
</tr>
<tr>
<td>Grassland Habitats(^b)</td>
<td>1998</td>
<td>58 (53)</td>
<td>73 (42)</td>
<td>1999</td>
<td>2097 (27)</td>
<td>37 (29)</td>
<td>2000</td>
<td>2285 (39)</td>
<td>40 (53)</td>
</tr>
<tr>
<td>Total</td>
<td>1998</td>
<td>110</td>
<td>172</td>
<td>1999</td>
<td>7667</td>
<td>129</td>
<td>2000</td>
<td>5826</td>
<td>76</td>
</tr>
</tbody>
</table>

\(^a\) Edge Habitats – right-of-way, wetland margins, and odd areas.
\(^b\) Grassland Habitats – pasture lands, hayfields, dense nesting cover.
\(^c\) Area of each habitat type searched.
Figure 2.1. Nesting habitat preference for northern pintails and mallards in an agricultural landscape in southern Saskatchewan, 1999, (A) using apparent number of nest found and (B) using number of nests found adjusted for daily survival rates (DSRs) and mean ages of nests when found. Error bars represent 95% Bonferroni adjusted confidence intervals.
stubble less than its availability ($\chi^2 = 6.00$, $P < 0.05$, Fig. 2.2). Nesting mallards did not use habitats in proportion to their availability in 1999 ($\chi^2 = 162.82$, $P < 0.001$, Fig. 2.1) or 2000 ($\chi^2 = 132.46$, $P < 0.001$, Fig. 2.2). Mallards nested in stubble significantly less than its availability and nested in edge and grassland habitats more than their availability. The differences between apparent nest numbers and adjusted nest numbers for DSRs and mean nest ages when found were large (Table 2.2), but analyses based on adjusted nest numbers only resulted in 2 changes in habitat preferences. First, pintails shifted from no preference to showing a preference for stubble in 1999 (Fig. 2.1). Second, mallards shifted from nesting for grassland habitat more than its availability to nesting in grassland habitat in proportion to its availability in 1999 (Fig. 2.1), but it is still obvious that they strongly avoid nesting in crop stubble.

**Nest-Site Characteristics and Nest Initiation Dates**

VORs were significantly different between species ($F_{1,751} = 81.21$, $P < 0.001$), among habitat types ($F_{2,751} = 244.01$, $P < 0.001$) and their interaction ($F_{2,751} = 5.44$, $P < 0.01$). Pintails consistently selected nest sites with lower VORs than mallards in crop stubble (difference between LSMEANS = -0.71 ± 0.21 dm, $t_1 = 3.43$, $P < 0.01$), edge habitats (-1.35 ± 0.30 dm, $t_{751} = 4.41$, $P < 0.001$), and grassland habitats (-1.59 ± 0.17 dm, $t_{751} = 9.49$, $P < 0.001$; Fig. 2.3). DISTWET varied among habitat types ($F_{1,749} = 6.65$, $P < 0.01$) but did not differ between species ($P = 0.41$) or habitat type by species interaction ($P = 0.21$, Fig. 2.4). Median nest initiation dates and interquartile ranges were similar among species and cultivation ($P > 0.35$, Fig. 2.5).
Figure 2.2. Nesting habitat preference for northern pintails and mallards in an agricultural landscape in southern Saskatchewan, 2000, (A) using apparent number of nest found and (B) using number of nests found adjusted for daily survival rates (DSRs) and mean ages of nests when found. Error bars represent 95% Bonferroni adjusted confidence intervals.
Table 2.2. Comparisons of apparent nest numbers (average nest age when found) and adjusted nest numbers for pintails and mallards in southern Saskatchewan 1999-2000.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>1999</th>
<th></th>
<th></th>
<th>2000</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pintail</td>
<td>Mallard</td>
<td></td>
<td>Pintail</td>
<td>Mallard</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Apparent</td>
<td>Adjusted(^c)</td>
<td>Apparent</td>
<td>Adjusted(^c)</td>
<td>Apparent</td>
<td>Adjusted(^c)</td>
</tr>
<tr>
<td>Crop Stubble</td>
<td>87 (10.2)</td>
<td>198</td>
<td>36 (9.8)</td>
<td>79</td>
<td>32 (7.1)</td>
<td>105</td>
</tr>
<tr>
<td>Edge Habitats(^a)</td>
<td>5 (7.3)</td>
<td>7</td>
<td>38 (6.8)</td>
<td>55</td>
<td>4 (5.5)</td>
<td>7</td>
</tr>
<tr>
<td>Grassland Habitats(^b)</td>
<td>37 (10.6)</td>
<td>50</td>
<td>52 (10.1)</td>
<td>69</td>
<td>40 (12.5)</td>
<td>121</td>
</tr>
</tbody>
</table>

\(^a\) Edge Habitats – right-of-way, wetland margins, and odd areas.
\(^b\) Grassland Habitats – pasture lands, hayfields, dense nesting cover.
\(^c\) Adjusted = apparent/DSR\(^a\), where DSR = daily survival rate, \(a\) = mean age of nests when found.
Figure 2.3. Visual Obstruction Readings (VOR) of pintail and mallard nest sites in crop stubble, edge, and grassland habitats type in southern Saskatchewan, 1999-2000. Error bars represent 95% confidence intervals.
Figure 2.4. Distance to nearest wetland (DISTWET) of pintail and mallard nests in crop stubble, edge and grassland habitat type in southern Saskatchewan, 1998-2000. Error bars represent 95% confidence intervals.
Figure 2.5. Minimums, maximums, medians, and interquartiles of estimated nest initiation dates for northern pintails and mallards and crop stubble cultivation dates in southern Saskatchewan, 1998-2000.
Nest Success

We located 1607 nests, of which 1257 were used to generate DSR estimates for habitat-year combinations. We excluded 350 nests from nest success analyses because of concurrent studies of renesting (n = 180) and brood survival (n = 13), investigator caused abandonment (n = 125) or damage (n = 27), or no fates were determined (n = 5). DSRs differed among years (χ²₂ = 49.23, P < 0.001) and habitat types (χ²₂ = 37.36, P < 0.001; Table 2.3). Overall, DSRs in crop stubble were lower (mean NS = 2.0%, 95% CI = 1.1-3.8%) than edge habitats (mean NS = 10.0%, 95% CI = 8-13%, χ²₁ = 6.52, P < 0.001) and grassland habitats (mean NS = 15%, 95% CI = 13-18%, χ²₁ = 33.72, P < 0.001; Table 2.3). In general, DSRs in 1999 were higher (mean NS = 25%, 95% CI = 21-29%, χ²₁ = 48.91, P < 0.001) than DSRs in 1998 and 2000 combined. Most nests (46-83%) failed due to predation in all year-habitat combinations; however, 20-33% of nests in crop stubble were destroyed by spring cultivation operations (Table 2.4). Mayfield nest success estimates in crop stubble excluding nests destroyed by spring cultivation operations were <1% (95% CI = <1-6%), 6% (95% CI = 4-16%), and <1% (95% CI = <1-4%) in 1998, 1999, and 2000, respectively.

Clutch Size

Mean clutch size was lower for pintails (7.68 ± 0.08 eggs, n = 266) than mallards (8.83 ± 0.07 eggs, n = 328, P < 0.001). Clutch size decreased seasonally (β = -0.04, SE = 0.00, P < 0.0001; Fig. 2.6), but the rate of seasonal decline did not differ between species (P = 0.09). Clutch size was similar among years (P = 0.81) for each species (P = 0.28) and the rate of seasonal decline did not differ among years (P = 0.65).
Table 2.3. Mayfield nest success estimates of upland nesting ducks in crop stubble, edge, and grassland habitats in southern Saskatchewan, 1998-2000. Daily survival rates (DSR) were converted to nest success estimates (NS) where NS = (DSR)^{1}, where 1 = 32, the sum of the average duration of laying and incubation for pintails.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>1998 NS% (95% CI)</th>
<th>N</th>
<th>1999 NS% (95% CI)</th>
<th>N</th>
<th>2000 NS% (95% CI)</th>
<th>N</th>
<th>Total NS% (95% CI)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop Stubble</td>
<td>&lt;1 (&lt;1-3)</td>
<td>51</td>
<td>4 (2-10)</td>
<td>92</td>
<td>&lt;1 (&lt;1-2)</td>
<td>30</td>
<td>2 (1-4)</td>
<td>173</td>
</tr>
<tr>
<td>Edge Habitats^a</td>
<td>6 (5-13)</td>
<td>137</td>
<td>16 (13-26)</td>
<td>139</td>
<td>3 (1-7)</td>
<td>66</td>
<td>10 (8-13)</td>
<td>342</td>
</tr>
<tr>
<td>Grassland Habitats^b</td>
<td>6 (5-12)</td>
<td>158</td>
<td>37 (34-48)</td>
<td>251</td>
<td>6 (4-8)</td>
<td>333</td>
<td>15 (13-18)</td>
<td>742</td>
</tr>
<tr>
<td>Total</td>
<td>6 (4-8)</td>
<td>346</td>
<td>25 (21-29)</td>
<td>482</td>
<td>5 (4-6)</td>
<td>429</td>
<td>11 (10-13)</td>
<td>1257</td>
</tr>
</tbody>
</table>

^a Edge Habitats – right-of-way, wetland margins, and odd areas.
^b Grassland Habitats – pasture lands, hayfields, dense nesting cover.
Table 2.4. Percentages and numbers (N) of upland duck nests lost to various failure sources in southern Saskatchewan, 1998-2000, excluding nests that were damaged or abandoned due to investigator activity.

<table>
<thead>
<tr>
<th>Year/Habitat</th>
<th>Predation</th>
<th>Agriculture</th>
<th>Snow</th>
<th>Flooding</th>
<th>Abandonment</th>
<th>Unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crop Stubble</td>
<td>59 (30)</td>
<td>33 (17)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td></td>
</tr>
<tr>
<td>Edge Habitats&lt;sup&gt;a&lt;/sup&gt;</td>
<td>70 (92)</td>
<td>6 (6)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>6 (6)</td>
<td></td>
</tr>
<tr>
<td>Grassland Habitats&lt;sup&gt;b&lt;/sup&gt;</td>
<td>70 (111)</td>
<td>&lt;1 (1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>8 (12)</td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crop Stubble</td>
<td>46 (42)</td>
<td>25 (23)</td>
<td>7 (6)</td>
<td>0 (0)</td>
<td>2 (2)</td>
<td></td>
</tr>
<tr>
<td>Edge Habitats</td>
<td>57 (79)</td>
<td>2 (3)</td>
<td>2 (3)</td>
<td>1 (2)</td>
<td>4 (5)</td>
<td></td>
</tr>
<tr>
<td>Grassland Habitats</td>
<td>37 (93)</td>
<td>0 (0)</td>
<td>2 (6)</td>
<td>1 (3)</td>
<td>2 (5)</td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crop Stubble</td>
<td>47 (14)</td>
<td>20 (6)</td>
<td>13 (4)</td>
<td>0 (0)</td>
<td>17 (5)</td>
<td></td>
</tr>
<tr>
<td>Edge Habitats</td>
<td>83 (55)</td>
<td>0 (0)</td>
<td>5 (3)</td>
<td>0 (0)</td>
<td>6 (4)</td>
<td></td>
</tr>
<tr>
<td>Grassland Habitats</td>
<td>79 (263)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>1 (4)</td>
<td>4 (14)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>62 (779)</td>
<td>5 (56)</td>
<td>2 (22)</td>
<td>&lt;1 (10)</td>
<td>4 (53)</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Edge Habitats – right-of-way, wetland margins, and odd areas.

<sup>b</sup> Grassland Habitats – pasture lands, hayfields, dense nesting cover.
Figure 2.6. Regression of clutch size on nest initiation date for Northern pintails (squares and dashed line) and mallards (circles and solid line) nesting in southern Saskatchewan, 1998-2000.
DISCUSSION

My results support previous speculation that on a landscape level, crop stubble may act as an ecological trap for nesting pintails (Miller and Duncan 1999). The increasingly common agricultural practice of leaving crop stubble over winter on the prairies has created an abundance of crop stubble habitat in the Canadian prairies. Unfortunately, this crop stubble serves as an ecological trap, which appears to be especially detrimental and largely unique to nesting pintails. I initially predicted nest success in crop stubble would be low due to catastrophic nest losses due to farm machinery during spring cultivation. However, only 20-33% of nests in crop stubble failed due to spring cultivation. Nest success in crop stubble is abysmal largely due to high rates of nest predation, not spring cultivation. Low nest success coupled with lower propensity to renest than mallards (Chapter 5) may partially explain the persistently low pintail population levels and only a meager response to improved wetland conditions in recent years.

Most (51%) pintail nests I found were in crop stubble and generally pintails nested in suitable habitats in proportion to their availability on the landscape (Fig. 2.1, 2.2). In contrast, most mallard nests were located in edge and grassland habitats, and they nested in habitats with dense cover in greater proportion to their availability and avoided crop stubble (Fig. 2.1, 2.2). My results suggest that pintails likely do not use fall-tilled habitats (1 nest/1066ha searched) for nesting, thus the elimination of fall tillage has created additional “attractive” nesting habitat for pintails. The proportion of pintail nests I found in crop stubble were similar to 51-57% and 45% of pintail nests in cropland reported by Klett et al. (1988) and Greenwood et al. (1995), respectively. Although, Klett et al. (1988) and Greenwood et al. (1995) found that pintails nested in cropland more frequently than mallards, they reported
pintails did not use habitats in proportion to their availability, but had greater relative preference rankings for planted cover, brush, and road right-of-way habitats than cropland. A likely explanation for the differences in habitat use I observed for pintails is that Klett et al. (1988) defined cropland as annually tilled fields or grain or row crops and made no distinction between fall-tilled areas and standing crop stubble. Because pintails likely do not use fall-tilled habitats for nesting, they probably underestimated the relative use of cropland by pintails. Although, Greenwood et al. (1995) made a distinction between fall-tilled and standing crop stubble habitats and excluded fall-tilled habitats from their analysis, several of their area-year combinations did not have any cropland that was suitable for nesting.

An inherent problem in determining habitat preference from habitat use and availability data is that results may be dependent upon what the researcher deems available to the animal (Johnson 1980, Thomas and Taylor 1990) and the choice of statistical methods used by the researcher (Alldredge and Ratti 1986). Consideration also must be given to the implications of spatial scale in habitat selection studies (Johnson 1980). Given the hierarchical nature of habitat selection (Johnson 1980), my estimates of nesting habitat preference for pintails are likely biased because I selected a highly agricultural landscape within the Prairie Pothole Region (PPR) to examine pintail nest site selection. The females I encountered in my study had previously selected southern Saskatchewan over other breeding areas in the PPR or Alaska (Grand et al. 1997). Within southern Saskatchewan, females had previously selected to settle in a highly agricultural landscape over landscapes with greater proportion of grassland habitats. Because I was unable to examine nest site selection on multiple spatial scales, inferences derived from my results regarding the continental population of pintails should be made with caution.
Given that pintails select nest sites with little cover or concealment relative to mallards (Fig. 2.3), the sparse vegetative structure of crop stubble is a likely proximate stimuli used by pintails when nesting in crop stubble. Ultimately, females should choose nest sites or adopt reproductive strategies that maximize their lifetime reproductive output (Rohwer 1992, Martin 1993). Although successful duck nests are often better concealed than unsuccessful nests (Hines and Mitchell, 1983, Crabtree et al. 1989, Clark and Shutler 1999), greater concealment might impose survival costs to females attending the nests (Götmark et al. 1995). Open nest sites may decrease risks of female predation by mammalian predators because females have a greater line of sight to see and avoid mammalian predators, but might increase the risk of avian predation on females (see Chapter 4). I suggest that recent anthropogenic habitat changes may have altered the composition of the predator community such that avian predators are relatively more important predators of pintails in Saskatchewan than during the evolutionary past.

My nest success estimates exhibited large spatial and temporal variation, but 7 of 9 year-habitat estimates were below the threshold level of 15% thought necessary to maintain pintail and mallard populations (Cowardin et al. 1985, Klett et al. 1998; Table 3). I was unable to examine nest success for pintails exclusively, but I pooled estimated across all dabbling ducks to obtain sound estimates of productivity in each habitat type. Consistent with recent previous studies (Higgins 1977, Klett et al. 1988, Greenwood et al. 1995), my nest success estimates in crop stubble were substantially lower (<1-4% vs. 6-37%) than the surrounding habitats with greater cover.

I was unable to test effects of patch size on DSRs due to lack of replication and small numbers of nests, but my results for nests in similar habitat structure tend to support the
hypothesis that DSRs are positively related to patch size (Clark and Nudds 1991, Sovada et al. 2000). DSRs were lower in edge habitats compared to larger blocks of contiguous grassland cover in 2 of 3 years (Table 2.3), likely because of edge habitats are travel corridors (Bider 1968) and preferred foraging sites (wetland margins) of striped skunks (Lariviere and Messier 1998) and perhaps raccoons.

My prediction based on the ecological trap hypothesis was that most nests in crop stubble would be destroyed by farm machinery during spring cultivation. That prediction was clearly wrong, as only 20-33% of nests in crop stubble failed due to tillage. My estimates were lower than the 41-57% and 37% reported by Milonski (1958) and Klett et al. (1988), respectively, perhaps due to differences in spring seeding practices. Unlike conventional seeded fields that are tilled before seeding, approximately 35% of the landowners on my study area practiced zero-till seeding where seed and fertilizer are placed directly into the soil with specialized air drills that minimize disturbance to the soil and existing stubble. One pass, zero-till seeding with air drills with $\geq 12$-inch row spacing allowed 34% of artificial nests to survive, compared to $< 1$% of nests that survived conventional seeding practices where crop stubble is tilled first and seeded during a second pass (Richkus and Rohwer, unpublished data).

Nest success estimates in crop stubble were much lower than surrounding habitats, but nest failures due to farm machinery account for little of this difference. I was surprised to find such high levels of predation in crop stubble (Table 4), however, stubble supported high densities of small mammals ($Microtus$ spp. and $Peromyscus$ spp.), which may have attracted predators to this habitat and increased the likelihood of duck nest predation. Red fox and
raccoons are not only major predators of duck nests (Sargeant et al. 1998), but are also frequent predators of *Microtus* spp and *Peromyscus* spp. (Lin and Batzli 1995).

My mean pintail clutch size (7.7 eggs) was higher than 6.9 eggs and 7.2 eggs reported by Duncan (1987a) and Guyn and Clark (2000) in Alberta, but similar to estimates from Manitoba and Alaska (8.0 eggs; Sowls 1955, 7.6 eggs; Flint and Grand 1996). Although pintails laid smaller clutches than mallards, the rate of seasonal decline was similar between species suggesting the same factors govern this trend for both species (see Rohwer 1992). The rate of season decline in clutch size I observed for pintails (0.04 eggs per day) was much less than the rate of seasonal decline observed for pintails in Alaska (0.09 eggs per day; Flint and Grand 1996).

**MANAGEMENT IMPLICATIONS**

I strongly agree with the recommendations of Miller and Duncan (1999) that management programs to facilitate pintail recovery should be targeted at increasing nest success. Because pintails nesting in a highly agricultural landscape in southern Saskatchewan generally nest in habitats in proportion to their availability on the landscape, habitat programs that protect existing mixed-grass prairie habitat or encourage ranching practices that provide productive pintail nesting habitat will likely benefit nesting pintails. However, there is considerable evidence that such programs may only produce a moderate improvement in nest success at the scale dictated by wildlife funding (Clark and Nudds 1991, McKinnon and Duncan 1999, Sovada 2000). Changes in agricultural policy that would provide funding and aim to restore vast areas of grassland in the Canadian prairie similar to the Conservation Reserve Program in the U.S. would likely have the greatest benefit to nesting pintails (Reynolds et al 1994, Reynolds et al. 2001). In addition, agricultural programs that encourage
zero-till seeding practices with wide row spacing (Richkus and Rohwer, unpublished data) or fall-seeded crops (J. Devries, Institute for Wetlands and Waterfowl Research, unpublished data) in areas with high pintail densities also may prove beneficial.

Because I observed such high rates of nest predation, especially in crop stubble, I believe that managers cannot ignore lethal predator removal as a supplement to habitat programs. Recent studies in North Dakota have shown that lethal predator removal can dramatically increase duck nest success (Hoff 1999, Garrettson and Rohwer 2001). Although these studies were conducted in areas with generally higher grassland cover (10-69%) than my study site, data suggests similar increases can be achieved in a highly agricultural landscape with a strong trapping effort (V. Lester, Delta Waterfowl and Wetlands Research Station, unpublished data). However there is no guarantee that predator management will increase pintail nest success in crop stubble habitats and may only result in shifting the cause of nest failures from predation to cultivation. Predator management may be most effective in landscapes with high wetland densities and grassland cover to attract breeding ducks, but where nest success remains low due to predation.

LITERATURE CITED


CHAPTER 3. RENESETTING ECOLOGY OF NORTHERN PINTAILS

For most prairie nesting dabbling ducks (*Anas* spp.), successive wet years on the prairies during the mid to late 1990s have resulted in population improvements to levels that exceeded the objectives set by the Northern American Waterfowl Management Plan (NAWMP; United States Fish and Wildlife Service [USFWS] 2000). For example, mallards (*A. platyrhynchos*) rebounded from 4.9 million breeding individuals in 1985, to a near record high of 10.8 million in 1999 (USFWS 2000). Unfortunately, the continental population of northern pintails (*A. acuta*; hereafter pintails) has failed to respond as expected to improved wetland habitat conditions on the prairies and has shown only a modest recovery from the record low of 1.8 million in 1991 (USFWS 2000). In 1999, the pintail breeding population of 3.1 million was 30% below the long-term average and pintails were the only species of dabbling duck below NAWMP population goals (USFWS 2000).

Waterfowl often suffer high rates of nest failure, largely due to predation (Keith 1961, Higgins 1977, Klett et al. 1988, Greenwood et al 1995), but also due to agricultural practices such as tillage and haying (Milonski 1958, Klett et al 1988, Higgins 1977, Greenwood et al. 1995). Several aspects of pintail nesting ecology may make their nests especially vulnerable to failure. Pintails nest early in the season (Higgins 1977, Duncan 1987, Greenwood et al. 1995, Grand et al. 1997) and are therefore, more vulnerable to spring snow (Krapu 1977, Greenwood et al. 1995) and predation (Greenwood et al. 1995, Beauchamp et al. 1996) than later nesting species. Pintails also have a higher propensity to nest in sparse cover than other ducks and frequently nest in crop stubble (Milonski 1958, Keith 1961, Stoudt 1971, Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Chapter 1). Nest success in cropland tends to be lower than the surrounding grasslands due to direct losses from tillage (Milonski 1958,
Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Chapter 1) and higher rates of predation (Chapter 1). Renesting, the laying of a replacement clutch following failure of a previous nesting attempt (Sowls 1955), is a common reproductive strategy that allows female ducks to compensate for high nest failure rates and to increase their seasonal reproductive success (Cowardin and Johnson 1979).

Because pintail nests may be at a greater risk of failure than other ducks, knowledge of pintail renesting rates and factors that affect renesting propensity are important to accurately model productivity (Carlson et al. 1993), and develop reliable life-cycle models (Flint et al. 1998). Miller and Duncan (1999) emphasized that field studies examining factors affecting pintail recruitment, especially in cropland, are critical to provide data to increase the predictive power of these models (Carlson et al. 1993, Flint et al. 1998) to evaluate pintail management. My primary objectives were to examine the influence of year (1998, 1999, 2000), female age (second-year, after second-year), date of clutch loss, incubation stage at clutch loss, and female body condition (body mass adjusted for structural size, date, and year of capture) on pintail renesting propensity and renest intervals. I also examined changes in clutch size among successive nesting attempts.

**STUDY AREA**

I conducted research from April to July during 1998-2000 on a 16,576 ha (64 square-mile) block on the edge of the Missouri Coteau in south-central Saskatchewan (49°35’ N, 104°29’ W), centered about 10 km south and 40 km west of the town of Weyburn, SK. Topography ranged from gently rolling pastures in the southwest to relatively flat cropland in the northeast. Wetlands interspersed in these habitats ranged from small ephemeral basins (< 1 ha) to a large (approx 290 ha) semi-permanent basin. Approximately 13,095 ha (79%) were
dominated by cereal grain and oil-seed agriculture, primarily spring wheat (*Triticum spp.*) and canola (*Brassica spp.*). During my study, 81-89% of the cropland was left in crop stubble during the winter; the remaining cropland was tilled in the fall leaving bare dirt. Other lands in the study area were pastures, hayfields, pond margins, road right-of-ways, odd areas (small areas of grass ≤ 2 ha found in cropland such as rock piles and fence rows), and 256 ha of nesting cover planted under the NAWMP (USFWS et al. 1994). Wetland densities were 27% and 30% below the long-term average for this region in 1998 and 2000, and 26% above the long-term average in 1999 (USFWS 2000). This study site was selected because of consistently high pintail breeding pair densities determined from the Canadian Wildlife Service (CWS) May counts (USFWS 2000) and a large proportion of the cropland was left over winter in stubble. I believe that this study site is typical of much of the pintail’s prairie breeding range.

**METHODS**

**Female Capture, Radiomarking, and Radiotelemetry**

I searched all upland habitats in randomly assigned quarter sections starting in late April and ceasing in late June in 1998 and early July in 1999 and 2000. Searching was conducted between 0800 and 1400 hrs when females were most likely to be present on incubation and laying stage nests (Gloutney et al. 1993). Waterfowl nests in grassland cover were located by systematically dragging a 70 m chain between two ATVs (Higgins et al. 1977, Klett et al. 1986). Due to lower nest densities in stubble, sparser residual vegetation, and the large proportion of stubble on the study area, a 200 m cable was used to more efficiently search cropland. Nests and renests were marked with a 50 cm willow (*Salix spp.*) stick placed 1 m south and an individually numbered, 90 cm white lathe 20 m north of each nest. Global
Positioning System (GPS) coordinates were also recorded for all pintail nests. I recorded clutch size, egg size, and developmental stage (Weller 1956) for each nest. I captured pintail females from randomly selected nests between 2 and 20 days of incubation throughout the nesting season using a modified Weller trap (Weller 1957) or a mist net (2000 only). I measured culmen length (± 0.1 mm), left tarsus length (± 0.1 mm), left wing cord length (± 0.1 mm), and weight of (± 5 g) each female. I aged females as second-year (SY) or after second-year (ASY) using secondary covert feather markings (Duncan 1985). Each female was fitted with a USFWS aluminum leg band and a 5 g prong and suture radio transmitter (< 1% of body mass, Advanced Telemetry Systems, Isanti, MN) described by Mauser and Jarvis (1991) with a slightly modified attachment procedure (Peitz et al. 1995). Transmitters had mortality sensors and expected battery lives of 100 days. To minimize stress, each female was given a 0.2 ml subcutaneous injection of the anesthetic lidocane at the attachment site prior to the procedure. Total handling time averaged 13.9 minutes from the time I removed a female from the trap or net, measured and fitted her with a radio transmitter, and released her near the nest site following the procedure. All procedures in this study were approved by Louisiana State University Institutional Animal Care and Use Protocol (A98-3), and University of Saskatchewan Animal Care Committee (03622-AI) on behalf on the Canadian Council of Animal Care.

To initiate renesting, I removed clutches 3 days after radio attachment. I suspected that this 3-day acclimation period minimized radio effects on renest likelihood or interval (T. Arnold, Institute for Waterfowl and Wetlands Research, personal communication). If a nest was depredated or the female abandoned her nest before the end of the acclimation period, I used her first date when she was radiolocated off the nest as the start of the renest interval.
tracked radio-marked females a minimum of once daily using truck-mounted, dual, 4-element Yagi antennas unless road conditions prohibited access through the study area. I located females between the hours of 0800 and 1400 hours until a female was triangulated to the same location in potential nesting cover for 3 consecutive days (Paquette et al. 1997). If a female was in potential nesting cover for 3 consecutive days, I approached the location on foot and attempted to flush the female and find the nest. If a female was located in crop stubble scheduled to be cultivated within a few days, I approached the location immediately to avoid missing a renesting attempt. If a female flushed at a long distance from nesting cover and the observer could not locate the nest, I used a dog to increase the probability of finding her renest. A renest was defined as $\geq 1$ egg in a new nest site (Sowls 1955). Renest initiation date was calculated by subtracting the sum of clutch size and incubation stage from the date the renest was located. Renest interval, the number of days between the date of the unsuccessful termination of the previous clutch and initiation date of a renest, was calculated for each female. Distance between nest sites was recorded with a 200 m distance tape if $\leq 200$ m or GPS if $> 200$m. After renests were located I did not visit the nest again until the projected forth day of incubation, unless the radiolocation clearly indicated that the female was away from her nests. Females were allowed to lay a full replacement clutch, and their eggs were then taken on the fourth ($\pm 1$ day) day of incubation. Females were tracked until they could no longer be located or moved to molting areas. Telemetry from fixed-wing aircraft was conducted every 12 - 14 days to locate females that could not be found from the ground (Gilmer et al. 1981).
Statistical Analyses

Body Size and Condition. -- I conducted all statistical analyses using SAS statistical software (SAS Institute Inc. 1999). I indexed structural size using principle components analysis (PROC PRINCOMP) of the correlation matrix of the 3 morphological measures taken from captured females. I used the first principle component (PC1) scores as a composite measure of structural size for each female (Alisauskas and Ankney 1987). I regressed (PROC GLM) female body mass on PC1 and created a size-adjusted measure of condition by adding the overall mean body mass of all birds to her residual from the regression (Ankney and Afton 1988). I used an analysis of covariance (ANCOVA) to examine effects of year (1998, 1999, 2000), female age (SY or ASY), incubation stage at capture and date of capture on size-adjusted body mass. I used the residual for each female from the ANCOVA as a measure of year and date adjusted body mass (CONDITION). I used the adjusted body mass of each female as a measure of her condition in subsequent survival analyses (Dufour et al. 1993).

Renesting Propensity and Renest Intervals. -- I used logistic regression (PROC LOGISTIC) to examine effects of year (1998, 1999, 2000), female age (SY, ASY), female condition, date of clutch loss (DATE), and incubation stage at clutch loss (STAGE) on the probability of a female renesting once. I also examined a priori models with 2-way interaction terms. I started with a set of 46 a priori candidate models and used Akaike Information Criterion (AIC) with the small sample size adjustment (AICₖ) to rank models and select the most parsimonious, information rich model (Akaike 1985, Burnham and Anderson 1998, Anderson et al. 2000). I considered the model with the lowest AICₖ value the best approximating model and used differences in AICₖ between that model and every other model.
(ΔAIC<sub>C</sub>) to identify other likely models. Generally, models within 2 AIC<sub>C</sub> points of the best model exhibit strong support, therefore I presented results from competing models within 2 AIC<sub>C</sub> points of the best approximating model (Burnham and Anderson 1998). To assess model selection uncertainty, I calculated Akaike weights (w<sub>i</sub>), which indicated the relative likelihood of each competing model given the data (Burnham and Anderson 1998, Anderson et al. 2000). When I presented results from alternative models (i.e. 0 < ΔAIC<sub>C</sub> < 2), I used model averaging to combine results from similarly parameterized models to obtain an unconditional estimate of effect size and standard error for each parameter (Burnham and Anderson 1998, Anderson et al. 2000). Females that were depredated before renesting or that were not consistently located following radio attachment were excluded from further renesting analyses.

I used an ANCOVA to assess effects of year, female condition, DATE, and STAGE on renest interval. Renest interval was log-transformed to meet model assumptions of normality and homoscedasticity (Neter et al. 1996). I used a forward selection criterion and variables were added to the model if they were significant at an alpha level of 0.05. I tested all 2-way interactions among significant variables. Phillips and Tienhoven (1962) reported that the ovaries and oviduct reached near maximum reduction in mass by 6 - 8 days incubation. Therefore, I used piecewise regression (Neter et al. 1996) to further examine if the relationship between renest interval and STAGE differed between early (≤ 8 days) and late incubation (> 8 days). I did not examine relationships for multiple renest attempts due to low sample size.

Clutch Size. -- I used an ANCOVA to test the effects of year and date of nest initiation on clutch size. I used the residuals from the ANCOVA as measures of year and date adjusted
clutch size and used a paired $t$-test to compare differences in date adjusted clutch size between initial nests and renest of individual females. Nests were excluded from clutch size analyses if they were depredated before a full clutch was laid no eggs added in 2 days) or showed evidence of a partial depredation. Means are reported ± standard error unless otherwise noted.

**RESULTS**

**Body Size and Condition**

Mean body mass was 675.0 ± 4.1 g for 140 radiomarked females. PC1 explained 48.0% of the overall variation among the 3 morphologic variables. All factor loadings were positive and ranged from 0.54 (wing cord length) to 0.60 (culmen length). The regression of female body mass on PC1 scores showed a positive relationship ($\beta = 16.42$, SE= 3.11, $P < 0.001$, $r^2 = 0.17$). Female condition at time of capture differed between years ($F_{2,134} = 3.72$, $P < 0.05$), declined as the season progressed ($F_{1,134} = 39.96$, $P < 0.001$) and the rate of decline differed among years ($F_{2,134} = 4.12$, $P < 0.05$, Fig. 3.1). Condition was unrelated to female age or incubation stage at capture ($P > 0.05$).

**Renesting Propensity and Renest Intervals**

I radio-marked and removed clutches of 140 pintail hens, 28 in 1998, 71 in 1999, and 41 in 2000 (Table 3.1). Of these, 11 females were depredated before renesting and 14 females moved > 80 km off the study area or their radios failed so they so were excluded from renesting analyses. Overall renesting rates were 50%, 71%, and 41% in 1998, 1999, and 2000, respectively. Because clutches were taken throughout the nesting season, it is possible that some females were already incubating a renest clutch at the time of capture; therefore...
Figure 3.1. Relationship between female body condition (body mass adjusted for structural size) of northern pintails and nest initiation date in southern Saskatchewan, 1998-2000. (1998 – circles and dotted line, 1999 – squares and solid line, 2000 – triangles and dashed line).
Table 3.1. Number of radiomarked female pintails and renesting rates in a highly agricultural landscape in southern Saskatchewan, 1998-2000.

<table>
<thead>
<tr>
<th></th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number radiomarked</td>
<td>28</td>
<td>71</td>
<td>41</td>
<td>140</td>
</tr>
<tr>
<td>Depredated a</td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>Not Located b</td>
<td>3</td>
<td>8</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>Renested</td>
<td>(11 of 22)</td>
<td>(42 of 59)</td>
<td>(14 of 34)</td>
<td>58%</td>
</tr>
<tr>
<td>2 Renests c</td>
<td>(2 of 11) d</td>
<td>(12 of 35) d</td>
<td>(8 of 14) e</td>
<td>37%</td>
</tr>
<tr>
<td>3 Renests c</td>
<td>(0 of 2)</td>
<td>(1 of 22)</td>
<td>(1 of 6)</td>
<td>7%</td>
</tr>
</tbody>
</table>

a Females depredated before renesting and excluded from renesting analyses.
b Females that experienced radio failure or could not be located and excluded from renesting analyses.
c Includes only females monitored from the previous renesting attempt.
d Contained 2 continuation nests.
e Contained 4 continuation nests.
these renesting estimates are biased low. To minimize this bias, I reanalyzed the data, but only included females likely incubating first nests by limiting the sample to females with nest initiation dates prior to the earliest known renest initiation date each year (11 May 1998, 12 May 1999, and 14 May 2000). Renesting rates for likely first nesting females were 61% (n = 18), 90% (n = 30), and 61% (n = 21) in 1998, 1999, and 2000. Of females that renested, few made multiple renesting attempts (Table 3.1). Only 1 female in 1999 and 1 in 2000 initiated 3 renests. These 2 females lost their initial clutch early in the season and their multiple attempts included at least one continuation nest, the initiation of a replacement clutch in a new nest bowl without interruption to the laying sequence (Arnold and Rohwer 1991).

The best fitting logistic regression model to predict probability of renesting for pintails included year, DATE, and year by DATE interaction terms (Table 3.2). This model indicated that renesting propensity differed by year (adjustment to the intercept relative to 2000, $\beta_{1998} = 98.21$, SE = 78.60, $\beta_{1999} = -48.57$, SE = 39.70), was negatively associated with DATE ($\beta = -0.50$, SE= 0.28), and the year by DATE interaction term indicated that the rate of the seasonal decline in renesting propensity differed among years (adjustment to the slope relative to 2000, $\beta_{1998*date} = -0.72$, SE = 0.57, $\beta_{1999*date} = 0.36$, SE = 0.28; Fig. 3.2.). Four other alternate models ($\Delta AIC_c \leq 2$) included 1 or more of the following parameters: (1) female condition, (2) STAGE, and (3) female condition by DATE interaction. These models indicated that renesting propensity increased with female condition (averaged $\beta = 0.01$, SE= 0.01; Fig. 3.3), but one alternate model allowed the effect of female condition to vary with DATE (averaged $\beta_{condition*date} = -0.00$, SE= 0.00). Renesting propensity decreased with STAGE (averaged $\beta = -0.05$ SE= 0.07; Fig. 3.4).
Table 3.2. Models used to assess effects of year, age, date of clutch loss (DATE), incubation stage at clutch loss (STAGE), and female body condition (CONDITION) on the probability of renesting for northern pintails in southern Saskatchewan, 1998-2000. The best-fitting model has the lowest Akaike’s Information Criterion adjusted for small sample size (AIC\(_C\)). Only models with \(\Delta\text{AIC}_C \leq 2.00\) are listed.

<table>
<thead>
<tr>
<th>Model</th>
<th>(K^a)</th>
<th>(\Delta\text{AIC}_C^b)</th>
<th>(w^c_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>year, date, year*date</td>
<td>6</td>
<td>0.00</td>
<td>0.189</td>
</tr>
<tr>
<td>year, date, condition, year*date</td>
<td>7</td>
<td>0.05</td>
<td>0.184</td>
</tr>
<tr>
<td>year, date, condition, year<em>date, condition</em>date</td>
<td>8</td>
<td>0.73</td>
<td>0.131</td>
</tr>
<tr>
<td>year, date, condition, stage, year*date</td>
<td>8</td>
<td>1.92</td>
<td>0.072</td>
</tr>
<tr>
<td>year, date, stage, year*date</td>
<td>7</td>
<td>1.97</td>
<td>0.070</td>
</tr>
</tbody>
</table>

\(K^a\) = number of parameters.

\(\Delta\text{AIC}_C^b\) = The difference in value between AIC\(_C\) of the current model versus the best fitting model (year, date, year*date; AIC\(_C\) = 91.760).

\(w^c_i\) = Likelihood that the current model is the best among competing tested models (\(n = 46\)). Unlisted models (\(\Delta\text{AIC}_C > 2.00\)) account for the remaining 0.354 of model weights (\(w_i\)).
Figure 3.2. Predicted probability of renesting for northern pintails given date of clutch loss in southern Saskatchewan, 1998-2000. Prediction probabilities were generated from our best fitting model containing year, date of clutch loss (DATE), and year by DATE interaction terms.
Figure 3.3. Predicted probability of renesting for northern pintails given size female condition (size adjusted body mass) at the time of capture in southern Saskatchewan, 1998-2000. Date of clutch loss was held constant at the where the predicted probability of renesting = 0.50 each year.
Figure 3.4. Predicted probability of renesting for northern pintails given incubation stage at the time of clutch loss in southern Saskatchewan, 1998-2000. Date of clutch loss was held constant at the where the predicted probability of renesting = 0.50 each year.
Renest intervals for females that lost their clutch during incubation averaged 11.2 ± 0.6 days (range 7 – 28 days, n = 67) with no difference among years (P > 0.05). However, log renest interval increased with stage (β = 0.02, SE= 0.01, P = 0.047; Fig. 3.5) and decreased slightly with date (β = 0.01, SE= 0.00, P = 0.051; Fig.3.6). I found no evidence of separate slopes in renest interval between early (≤ 8 days) and late (> 8 days) incubation (P = 0.26). For females that made a second renest attempt, renest intervals for females that lost their clutch during laying (4.6 ± 1.1 days, n = 13) was lower than females that lost their clutch during incubation (11.3 ± 1.2 days, n = 9). Distance between nest sites averaged 605 ± 87 m and ranged from 14 to 3210 m. (Fig. 3.7). Sixty-nine percent of renests were within 500 m of the initial nest sites.

**Clutch Size**

Mean clutch size was 7.7 ± 0.1 eggs for 158 nests where a full clutch was produced. Clutch size did not differ among years or nesting attempts (P > 0.05), but declined seasonally (β = -0.06, SE = 0.01, P < 0.001). For 22 females that had a known initial clutch size and completed a renest clutch, clutch sizes adjusted for laying date were not significantly different between initial nests and renests (t_{21} = -0.03, P = 0.97).

**DISCUSSION**

My telemetry-based estimates of renesting rates for nest-trapped females likely incubating first nests were similar to 85% (11 of 13) of nest-trapped females reported by Guyn and Clark (2000) near Brooks, Alberta, but slightly higher than 56% (22 of 39) reported by Grand and Flint (1996a) on the Yukon-Kuskokwim (Y-K) Delta, Alaska. Grand and Flint (1996a) suggested that their estimate was likely biased low because some renesting attempts
Figure 3.5. Relationship between renest interval and incubation stage for northern pintails in southern Saskatchewan, 1998-2000. Date of clutch loss was held constant at the mean date of clutch loss (14 May). Renest intervals were back log-transformed.
Figure 3.6. Relationship between renest interval and date of clutch loss for northern pintails in southern Saskatchewan, 1998-2000. Incubation stage at clutch loss was held constant at the mean incubation stage clutch loss (8 days). Renest intervals were back log-transformed.
Figure 3.7. Distance between nest sites for northern pintails in southern Saskatchewan, 1998-2000.
could have gone undetected due to low nest attendance by laying females, low nest success, and the inability to monitor females that left the study area. Although I located females daily, unlike the 1 to 10 days by Grand and Flint (1996a), I too believe that my estimate may be biased low. Renests were often found late in the laying cycle, nest success in 1998 and 2000 was low, especially in crop stubble (Chapter 2), and nearly 80% of the study area was tilled over the nesting season, therefore it was possible that some renests went undetected. Duncan (1987) reported that only 4% (5 of 127) of color-marked and 0 of 17 radio-marked females renested in southern Alberta. Grand and Flint (1996a) suggested that Duncan (1987) underestimated renesting rates because detection and emigration rates of color-marked females were unknown. Additionally, recent work has revealed negative effects of backpack transmitters, such as used by Duncan (1987), on mallard nesting effort (Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997) and it is likely that those effects are similar for pintails.

From an evolutionary standpoint, one of the advantages of early nesting is an increased opportunity to renest (Rohwer 1992). Therefore, one would predict that early nesting species like pintails would be persistent renesters. Although most pintails renested, my data suggest that most females renest only once and rarely initiate multiple renests. My estimates of multiple renests by prairie-nesting female pintails in Saskatchewan were slightly higher (22 of 60 vs. 3 of 22) than sub-artic-nesting females on the Y-K Delta, Alaska (Grand and Flint 1996a). Arctic nesting pintails may have reduced renesting potential than prairie nesting pintails, likely due to a shorter nesting season (Calverley and Boag 1977). In contrast to pintails, 81% of mallards, a species with similar early nest initiation dates (Greenwood et al. 1995), renested and some females made up to 6 nesting attempts (Rotella et al. 1993).
Not surprisingly, I found a strong seasonal decline in renesting propensity. A similar relationship was found for pintails on the Y-K Delta, Alaska (Grand and Flint 1996a) and although their sample size was small, Guyn and Clark (2000) suggested renesting rate declined with date for pintails in Alberta. Seasonal declines in renesting rates have also been found for mallards (Krapu et al. 1983), gadwalls (A. strepera; Gates 1962), blue-winged teal (A. discors; Strohmeyer, 1967), and American coots (Fulica americana; Arnold 1993). I found that the degree of seasonal decline of pintail renesting propensity varied between years (Fig. 3.2). This effect was likely associated with annual and seasonal variation in water levels, which influenced the availability of foods to females. Similarly, mallard renesting propensity was affected by wetland abundance (Krapu et al. 1983, Cowardin et al. 1985). In 1998, pond numbers were low at the onset of nesting with little precipitation throughout the nesting season, possibly explaining the abrupt decline in the probability of renesting. In 1999, water was much more abundant due to a late spring snowstorm and frequent rainfall throughout the nesting season. Consequently, renesting persisted much later into the nesting season at a more gradual rate of decline. Pond numbers at the onset of nesting in 2000 were very similar to 1998, but remained fairly constant because of frequent precipitation.

A decrease in water levels or pond numbers and subsequent decrease in food availability may affect breeding females in 3 ways. First, a decrease in food availability may affect female ability to secure exogenous resources to form her renest clutch. Ducks typically have few reserves available for renesting and must rely on exogenous resources to form their renest clutch (Krapu 1974, 1981, Esler and Grand 1994). Second, a decrease in food availability may directly affect female condition. Although renesting pintails do not use endogenous reserves for clutch formation (Esler and Grand 1994), Guyn and Clark (2000)
suggested female pintails may need to have some threshold of stored reserves before
renesting, possibly to overcome the energetic cost of incubation (Afton and Paulus 1992),
which may become more apparent later in the nesting season. Finally, a decrease in water
levels or pond numbers may act as a proximal cue for females to terminate breeding after an
unsuccessful nest. Females may assess future resources available for brood rearing and trade
off current reproductive potential (i.e. renesting) for greater future reproductive potential (i.e.
survival).

Female condition declined with nest initiation dates and the rate of decline varied
between years (Fig. 1). Grand and Flint (1996a) found a similar relationship between body
mass and nest initiation date. However, Duncan (1987) and Guyn and Clark (2000) failed to
find a significant relationship between body mass and nest initiation dates for wild or captive
pintails. Interestingly, Duncan (1987) and Guyn and Clark (2000) conducted fieldwork near
Brooks, Alberta, on managed wetland complexes where water levels were relatively stable.
The seasonal decline in condition I found in my study likely implies that females in better
condition nest earlier to maximize recruitment potential (Rohwer 1992) when habitat
conditions are unpredictable. I suspect the difference in rates of decline in female condition
among years was caused by annual and seasonal variation in pond numbers. Interestingly, I
failed to find a negative relationship between female condition and incubation stage at
capture, which is common for most waterfowl (Harris 1970, Krapu, 1981, Gatti 1983, Afton
and Paulus 1992). Feeding is reduced during incubation and therefore females must use
endogenous reserves for body maintenance and heat exchange to the eggs (Gatti 1983). The
lack of a negative relationship between female condition and incubation stage implies that
female pintails may have lower incubation constancy, allowing females to feed more
frequently to maintain body mass throughout incubation. Conversely, pintails may be more efficient foragers during incubation recesses that other ducks.

My mean pintail renest interval estimate of $11.2 \pm 0.6$ days was similar to $11.3 \pm 1.5$ days reported by Grand and Flint (1996a) and $9.6 \pm 0.6$ days reported by Duncan (1987) for captive-reared pintails, but shorter than $18.7 \pm 2.7$ days reported by Guyn and Clark (2000) for nest-trapped females. Renest intervals were shorter for captive mallards when food availability was high (Swanson et al. 1986), therefore variation among studies might reflect differences in food availability or simply reflect differences in field methods. I found no relationship between female condition and renest interval consistent with Krapu’s (1974, 1981) findings that renesting ducks typically have few endogenous nutrient reserves and do not use reserves for renest clutch production (Esler and Grand 1994). Pintail renest intervals were positively correlated with incubation stage at clutch loss (Fig 3.5). Similar relationships have been found for mallards (Sowls 1955, Swanson et al. 1986) and blue-winged teal (Strohmeyer 1967), likely due to the regression of ovaries during incubation. Phillips and Tienhoven (1962) reported that the ovary and oviduct reached near maximum reduction in mass by 6 – 8 days incubation, however I found no evidence of differing rates of increase of renest interval with stage between early ($\leq 8$ days) and late incubation (>8 days). I suspect this lack of a change in slope between early and late incubation implies that other physiological factors that were not reflected in my metric of female condition, possibly affected renest intervals. Pintail renest intervals were also weakly negatively correlated with DATE (Fig. 3.6). There are 3 potential explanations for the seasonal decline in renest intervals. First, late spring snow storms on 10 May and 11 May in 1999 and 2000 respectively, may have increased the renest intervals of females that lost their clutch prior to
or during the snow. During periods of prolonged cold, females likely divert metabolic energy from ovary and oviduct regeneration or clutch production to thermoregulation. Furthermore, type I, II, and III wetlands were frozen for 3 days (10 May – 13 May) during 1999, potentially limiting access to foods. However, the seasonal decline in renest interval was similar among years and was evident in 1998 when there was not a late spring snowstorm. Second, there is likely some proximal cue associated with date, such as photoperiod whereby females shorten renest intervals toward the end of the nesting season. Finally, food availability may increase seasonally, which allows faster ovary and oviduct regeneration by females. Regardless of the mechanism, ultimately, late renesting and longer renest intervals results in later hatch dates which translates to lower brood and duckling survival (Grand and Flint 1996b, Guyn and Clark 1999).

Seasonal declines in pintail clutch sizes have been also reported by (Flint and Grand 1996, Duncan 1987, Guyn and Clark 2000) and many researchers have hypothesized that the decline in part is due to smaller clutches laid by renesters. Although renest clutches were smaller than initial clutches, after correcting for nest initiation date, clutch size was similar between initial nests and renests. Similar relationships were found for captive-reared mallards (Batt and Prince 1979), captive-reared pintails (Duncan 1987) and American coots (Arnold 1993) suggesting that date and not renesting is responsible for seasonal declines in clutch size.

Mean distance between nest sites was further in my study than the 276, 390, and 258 m reported by Grand and Flint (1996a), Duncan (1987), and Sowls (1955), respectively. The longer distances I observed may be due to the habitat composition of my study area. Because I worked in a highly agricultural landscape, and pintails rarely nest in tilled habitats (Chapter
1), females might have had to move longer distances to find suitable nesting habitat after tillage of crop stubble.

**MANAGEMENT IMPLICATIONS**

Most ducks select nest sites in grassland habitats and avoid nesting in cropland habitats (Cowardin et al. 1985, Greenwood et al. 1995, Chapter 2). Furthermore, later nesters like blue-winged teal (*A. discors*) and gadwall (*A. strepera*), have little opportunity to nest in crop stubble because the chronology of seeding for cereal grains and oil-seed crops is ahead of their nesting chronology. However, pintails have a higher propensity to nest in sparse cover, including cropland, relative to other ducks (Milonski 1958, Keith 1961, Stoudt 1971, Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Chapter 2), where their nests are at a greater risk of failure due to tillage and predation. Therefore, knowledge of factors affecting renesting is essential to modeling pintail productivity and developing a reliable lifecycle model. Unfortunately, spring tillage may substantially impact pintail hen success in a highly agricultural landscape because of direct losses from machinery during spring cultivation. Mean tillage dates on my study area of 8 May, 16 May and 9 May in 1998, 1999, and 2000 respectively, should give females ample time to renest, but a late spring from an agricultural standpoint or late tillage of summer fallow could considerably decrease pintail productivity. Annual variation in pintail renesting propensity appeared to be related to wetland abundance, which may affect food availability to females (Krapu et al. 1983, Cowardin et al. 1985). Therefore, management programs that protect type I and II wetlands, which are important to breeding female pintails (Smith 1995), may increase pintail hen success. However, pintails do not appear to be as persistent renesters as mallards and management programs to increase pintail productivity should primarily be focused on increasing nest success.
LITERATURE CITED


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CHAPTER 4. SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF FEMALE NORTHERN PINTAILS

For most prairie nesting dabbling ducks (*Anas* spp.), successive wet years on the prairies during the late 1990s have resulted in population improvements to levels that exceeded the objectives set by the Northern American Waterfowl Management Plan (NAWMP; United States Fish and Wildlife Service [USFWS] 2000). For example, mallards (*A. platyrhynchos*) rebounded from 4.9 million breeding individuals in 1985, to a near record high of 10.8 million in 1999 (USFWS 2000). Unfortunately, the continental population of northern pintails (*A. acuta*; hereafter pintails) has failed to respond as expected to improved wetland habitat conditions on the prairies and has shown only a modest recovery from the record low of 1.8 million in 1991 (USFWS 2000). In 1999, the pintail breeding population (BPOP) of 3.1 million was 30% below the long-term average and pintails were the only species of dabbling duck below NAWMP population goals (USFWS 2000).

A key parameter affecting waterfowl population dynamics is female survival. Estimates of annual survival for female pintails are obtained from models (Brownie et al. 1985) based on direct band recoveries (Reinecker 1987, Hestbeck 1993). Although annual survival rates derived from banding are crucial for productivity and population modeling (Carlson et al. 1993, Flint et al. 1998), they do not allow survival to be partitioned into segments of the annual cycle or identify cause-specific sources of natural mortality. Studies that estimate survival during specific stages of the annual cycle are crucial to improve our understanding of waterfowl population regulation, develop accurate population models, and improve management decisions (Johnson et al. 1992).

During the last decade, several studies have assessed winter survival of female pintails (Migoya and Baldassarre 1995, Miller et al. 1995, Cox et al. 1998). Miller et al. (1995)
estimated winter survival of adult females to be 0.87 in Sacramento Valley, California, the state that supports the largest wintering pintail population (Bellrose 1980). In Sinaloa, Mexico the winter survival estimate of 0.91 for female pintails was similarly high (Migoya and Baldassarre 1995). With the exception of survival estimates for southwestern Louisiana (Cox et al. 1998; immatures - 0.55, adults - 0.71), high telemetry-based estimates of winter survival for female pintails indicate that the lack of response of pintails to improved wetland habitat conditions does not appear to be solely related to winter survival of females.

Miller et al. (1995) noted that estimated survival for female pintails during the non-wintering periods (annual survival/ winter survival = 0.75) was lower than their winter survival estimate and suggested managers should examine breeding or migration periods for opportunities to achieve increases in female survival. Females often suffer greater mortality during the breeding season than other segments of the annual cycle due to increased vulnerability to mammalian and avian predation (Johnson and Sargeant 1977, Sargeant et al. 1984, Johnson et al. 1992). Unfortunately, data on the breeding season survival of female pintails are lacking, a data gap that was noted in recent productivity and population models (Carlson et al. 1993, Flint et al. 1998). My primary objectives were to estimate survival and cause-specific mortality of female pintails during the nesting season. I tested for variation in survival rates in relation to female age (second-year, after second-year), year (1998, 1999, 2000), and female body condition (body mass adjusted for structural size, date, and year of capture).

**STUDY AREA**

I conducted research from April to July during 1998 - 2000 on a 16,576 ha (64 square-mile) block on the edge of the Missouri Coteau in south-central Saskatchewan (49°35’ N,
Topography ranged from gently rolling pastures in the southwest to relatively flat cropland in the northeast. Wetlands interspersed in these habitats ranged from small ephemeral basins (< 1 ha) to a large (approx 290 ha) semi-permanent basin. Approximately 13,095 ha (79%) were dominated by cereal grain and oil-seed agriculture, primarily spring wheat (*Triticum spp.*) and canola (*Brassica spp.*). During my study, 81-89% of the cropland was left crop stubble during the winter; the remaining cropland was tilled in the fall leaving bare dirt. Other lands in the study area were pastures, hayfields, pond margins, road right-of-ways, odd areas (small areas of grass ≤ 2 ha found in cropland such as rock piles and fence rows), and 256 ha of nesting cover planted under the NAWMP (USFWS et al. 1994). Wetland densities were 27% and 30% below the long-term average for this region in 1998 and 2000, and 26% above the long-term average in 1999 (USFWS 2000). This study site was selected because of consistently high pintail breeding pair densities determined from the Canadian Wildlife Service (CWS) May counts (USFWS 2000) and the large proportion of the cropland that was left over winter in stubble. I believe that this study site is typical of much of the pintail’s prairie breeding range. Potential predators of pintail females in this area included: coyote (*Canis latrans*), red fox, mink (*Mustela vison*), northern harrier (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*), Swainson’s hawk (*B. swainsoni*), ferruginous hawk (*B. regalis*) and great horned owl (*Bubo virginianus*).

**METHODS**

**Female Capture, Radiomarking, and Radiotelemetry**

I captured pintail females from randomly selected nests between 2 and 20 days of incubation (Weller 1956) from April to June using a modified Weller trap (Weller 1957) or a
mist net (2000 only). I measured culmen length (± 0.1 mm), left tarsus length (± 0.1 mm), left wing cord length (± 0.1 mm), and weight (± 5 g) of each female. I aged females as second-year (SY) or after second-year (ASY) using secondary covert feather markings (Duncan 1985). Each female was fitted with a USFWS aluminum leg band and a 5 g prong and suture radio transmitter (< 1% of body mass, Advanced Telemetry Systems, Isanti, Minnesota, USA), described by Mauser and Jarvis (1991), but with a slightly modified attachment procedure (Peitz et al. 1995). Transmitters had mortality sensors and expected battery lives of 100 days. To minimize stress, each female was given a 0.2 ml subcutaneous injection of the anesthetic lidocane at the attachment site prior to the procedure. Total handling time averaged 13.9 minutes from the time I removed a female from the traps or nets, measured and fitted her with a radio transmitter, and released her near her nest site following the procedure. All procedures in this study were approved by Louisiana State University Institutional Animal Care and Use Protocol (A98-3), and University of Saskatchewan on behalf on the Canadian Council of Animal Care (03622-AI).

I monitored survival during an induced renesting study (Chapter 3), in which clutches were removed 3 days after transmitter attachment to initiate renesting. I tracked radio-marked females a minimum of once daily using truck-mounted, dual, 4-element Yagi antennas unless road conditions prohibited access through the study area. I located females between the hours of 0800 and 1400 hours (Gloutney et al. 1993) until they were triangulated to the same location in potential nesting cover for 3 consecutive days (Paquette et al. 1997). If a female was in potential nesting cover for 3 consecutive days, I approached the location on foot and attempted to flush the female and find the nest. If a female was located in crop stubble scheduled to be cultivated within a few days, I approached the location immediately to avoid
missing a renesting attempt. After renests were located I did not visit the nest again until the projected fourth day of incubation to remove the clutch, unless the radiolocation clearly indicated that the female was away from her nest. I tracked and assessed status (alive or dead) of females until they moved to molting areas or could no longer be located. I immediately retrieved carcasses and transmitters with activated mortality sensors and identified cause of death from physical evidence at the recovery site (Einarsen 1956, Sargeant et al. 1998) and appearance of the transmitter. Causes of female mortalities were classified as avian, red fox, collision with power line, or unknown. Telemetry from fixed-wing aircraft was conducted every 12 - 14 days to locate females that could not be found from the ground (Gilmer et al. 1981).

Statistical Analyses

Body Size and Condition. -- I conducted all statistical analyses using SAS statistical software (SAS Institute Inc. 1999). I indexed structural size using principle components analysis (PROC PRINCOMP) of the correlation matrix of the 3 morphological measures taken from captured females. I used the first principle component (PC1) scores as a composite measure of structural size for each female (Alisauskas and Ankney 1987). I regressed (PROC GLM) female body mass on PC1 and created a size-adjusted measure of condition by adding the overall mean body mass of all birds to her residual from the regression (Ankney and Afton 1988). I used an analysis of covariance (ANCOVA) to examine the effects of year (1998, 1999, 2000), female age (SY or ASY), incubation stage at capture, and date of capture on size-adjusted body mass. I used the residual for each female from the ANCOVA as a measure of year and date adjusted body mass (CONDITION). I used
the adjusted body mass of each female as a measure of her condition in subsequent survival analyses (Dufour et al. 1993).

Survival and Cause Specific Mortality. -- I used Cox (1972) proportional hazards regression generalized for staggered entry (PROC PHREG; Allison 1995) to test for differences in survival relative to female age (SY or ASY), year (1998, 1999, 2000), female condition and all 2-way interactions. I observed no mortalities within 7 days of release; therefore, I assumed stress from capture and handling had no effect on survival (Pollock et al. 1989) and females were entered into the model the day following release. I used 30 April as the origin and censored females if they were alive on 14 July when radio tracking ended. This interval was fully represented in all 3 years of the study. Females with radiotransmitter failure, or birds that emigrated from the study area were right censored the last day of observation. I assumed that right censorship was random and independent of fate of radiomarked females (Pollock et al. 1989). Furthermore, I assumed survival was independent among all females and that radiotransmitters had no effect on survival (Pollock et al. 1989). I also assumed that left censored individuals, due to staggered entry, had survival distributions similar to previously marked birds (Pollock et al. 1989). To arrive at my final model, I used backward selection and removed non-significant (P > 0.05) terms from the model starting with the highest order interactions. I used the product-limit method (Kaplan and Meier 1958) generalized for staggered entry to calculate periodic survival rates (Allison 1995).

Cause-specific mortality was defined as the probability of a female pintail dying from a given mortality. I estimated cause-specific mortality rates for each of the 4 mortality agents as if they were the only source of mortality. For each model, I treated mortalities from competing mortality agents as right censored the day of death. For these estimates of cause-
specific mortality, I assumed causes of mortality were independent. I did not perform tests for
effects of year and female age on cause-specific mortalities rates because no clear standard
exists by which to estimate variances for mortality rates of 0.0 (5 of 12 year-mortality agent
combinations), particularly with a staggered entry design (Davis et al. 2001). However, I
tested for differences in cause-specific mortality rates between mortality agents for years and
ages combined using a generalized chi-square hypothesis testing produce outlined by Sauer
and Williams (1989) in program CONTRAST (Hines and Sauer 1989). Means are reported ±
standard error unless otherwise noted.

RESULTS

Body Size and Condition

Mean body mass was 675.0 ± 4.1 g for 140 radiomarked females. PC1 explained
48.0% of the overall variation among the 3 morphologic variables. All factor loadings were
positive and ranged from 0.54 (wing cord length) to 0.60 (culmen length). The regression of
female body mass on PC1 scores showed a positive relationship (β = 16.42, SE= 3.11, P <
0.001, r² = 0.17). Female condition at time of capture differed between years (F2,134 = 3.72, P
< 0.05), declined as the season progressed (F1,134 = 39.96, P < 0.001) and the rate of decline
differed among years (F2,134 = 4.12, P < 0.05, Fig. 4.1). Condition was unrelated to female
age or incubation stage at capture (P > 0.05).

Seasonal Survival and Cause-Specific Mortality

I used fates of 140 radio-marked pintail females (28, 71, and 41 in 1998-2000) with
3,798 exposure days to estimate survival and cause-specific mortality from 30 April to 14
July. The overall survival rate for the 75 day period was 0.81 ± 0.05 (Fig. 4.2). I found no
evidence that the hazard function varied among years, or between ages, nor was it related to
Figure 4.1. Relationship between female body condition (body mass adjusted for structural size) of northern pintails and nest initiation date in southern Saskatchewan, 1998-2000. (1998 – circles and dotted line, 1999 – squares and solid line, 2000 – triangles and dashed line).

1998 – $Y = 763.39 - 2.45(DATE)$
1999 – $Y = 694.09 - 0.73(DATE)$
2000 – $Y = 742.04 - 1.42(DATE)$
Figure 4.2. Survival rate and 95% confidence intervals (30 Apr – 14 July, 75 days) of radiomarked female northern pintails in southern Saskatchewan, 1998-2000, considering all sources of mortality.
female condition at capture, or any 2-way interactions ($P > 0.12$). I documented 15 deaths due to avian predators ($n = 11, 73\%$), red fox ($n = 1, 7\%$) collision with a power line ($n = 1, 7\%$), and unknown causes ($n = 2, 13\%$, Table 4.1). Cause-specific mortality rates differed among agents ($\chi^2_3 = 10.54, P < 0.05$, Table 4.1), and were greater for avian predators than other mortality agents ($\chi^2_1 = 8.36, P < 0.01$).

**DISCUSSION**

My 75-day estimate for nesting season survival for female pintails is lower than winter survival estimates in California (Miller et al. 1995) and Mexico (Migoya and Baldassarre 1995), but slightly higher than winter estimates in southwestern Louisiana (Cox et al. 1998; Table 4.2). However, my 75-day interval was shorter than intervals for wintering studies (Table 4.2) suggest nesting season survival may be lower than winter. In addition, I suspect my estimate of survival during the nesting season is biased high because I monitored female survival during a concurrent study of induced renesting (Chapter 3). Days when radiomarked females were incubating a clutch were likely underrepresented relative to the population because clutches of radiomarked females were repeatedly removed in early incubation to assess renesting propensity. Kirby and Cowardin (1986) reported that survival of female mallards during incubation was lower than other periods during the nesting season, confirming previous speculation that females suffer high mortality rates while attending nests (Johnson and Sargeant 1977, Sargeant et al. 1984, Cowardin et al. 1985). That said, female pintail survival during the nesting season on my study area might be substantially lower than survival during the winter.

My 75-day estimate for female pintail survival during the nesting season was similar to spring and summer survival estimates for mallards in North Dakota, but slightly higher
Table 4.1. Number of mortalities (n) and interval (30 Apr – 14 July; 75 days) mortality rates (M) for female northern pintails (n = 140) in southern Saskatchewan, 1998-2000.

<table>
<thead>
<tr>
<th>Mortality Agent</th>
<th>n</th>
<th>M</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avian predator</td>
<td>11</td>
<td>0.14</td>
<td>0.04</td>
</tr>
<tr>
<td>Red fox</td>
<td>1</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Collision with power line</td>
<td>1</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Unknown causes</td>
<td>2</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>0.19</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Table 4.2. Survival rates (S ± SE) female pintails during the winter and female mallards and pintails during the breeding season from radiotelemetry studies.

<table>
<thead>
<tr>
<th>Season/Species</th>
<th>Region</th>
<th>Days</th>
<th>Age$^a$</th>
<th>S</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wintering</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Pintail</td>
<td>Mexico</td>
<td>107</td>
<td>HY, AHY</td>
<td>0.91</td>
<td>Migoya and Baldassarre 1995</td>
</tr>
<tr>
<td>Northern Pintail</td>
<td>California</td>
<td>180</td>
<td>AHY</td>
<td>0.87 ±0.03</td>
<td>Miller et al. 1995</td>
</tr>
<tr>
<td>Northern Pintail</td>
<td>Louisiana</td>
<td>147</td>
<td>AHY</td>
<td>0.71 ±0.05</td>
<td>Cox et al. 1998</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>HY</td>
<td>0.55 ± 0.07</td>
<td></td>
</tr>
<tr>
<td>Breeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mallard</td>
<td>North Dakota</td>
<td>153</td>
<td>SY, ASY</td>
<td>0.81</td>
<td>Cowardin et al. 1985</td>
</tr>
<tr>
<td>Mallard</td>
<td>Minnesota</td>
<td>169</td>
<td>AHY</td>
<td>0.71 ± 0.08$^b$</td>
<td>Kirby and Cowardin 1986</td>
</tr>
<tr>
<td>Northern Pintail</td>
<td>Saskatchewan</td>
<td>75</td>
<td>SY, ASY</td>
<td>0.81 ± 0.05</td>
<td>This study</td>
</tr>
</tbody>
</table>

$^a$ HY = hatch-year, AHY = after hatch-year, SY = second-year, ASY = after second-year.

$^b$ Standard error misreported in Kirby and Cowardin (1986) as 0.77.
than estimates for mallards in Minnesota (Table 4.2). Again, my 75-day interval was shorter than intervals in other studies on mallards (Table 4.2) suggesting female pintail survival over the entire breeding season may be lower than mallards.

I found no evidence that female survival differed among years, but nest success estimates (5-25%) varied dramatically on my study area between 1998-2000 (Chapter 2). The lack of an apparent positive correlation between female survival and nest success estimates is likely due to the preponderance of raptor mortality on females, which do not depredate duck eggs, while I suspect most nests were depredated by striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*), which typically do not capture females (Sargeant and Arnold 1984).

Unlike the wintering grounds, where immature females may suffer greater mortality rates due to increased vulnerability to hunting (Cox et al. 1998), I failed to detect a difference in survival rates between SY and ASY females. Swanson et al. (1986) reported ASY female mallards had a greater renesting propensity relative to SY females. Therefore, one could predict that ASY females might experience greater breeding season mortality than SY females because of more potential exposure days incubating a clutch when risk of predation is higher (Kirby and Cowardin 1986). However, I failed to detect an age-specific difference in renesting propensity for these radiomarked females (Chapter 3), potentially explaining the lack of an age effect on female survival. Conversely, one could predict ASY females may have greater survival than SY females due to previous encounters with and more experience eluding predators. However, my results suggest that females do not “learn” from previous encounters with predators, perhaps because their first encounter results in mortality. Therefore, large age-specific differences in annual survival between immatures and adults
likely occur during fall migration or hunting periods and not during the breeding season (Johnson et al. 1992, Cox et al. 1998).

Similar to previous studies on wintering female pintails (Migoya and Baldassarre 1995, Miller et al. 1995, Cox et al. 1998), I found no effect of body condition on survival during the breeding season. Although my sample consisted of randomly captured nest trapped females, females in my sample may have had a high measure of body condition relative to females that never initiated a nest. Cox et al. (1998) speculated that one reason for their failure to detect any effect of condition on winter survival is that females in the poorest condition never arrived on the wintering grounds because of mortality during fall migration. Likewise, the females in the poorest condition may never arrive on the breeding grounds because of mortality during spring migration. Alternatively, food availability on the breeding areas may allow females to maintain a body condition above any possible survival threshold.

I found that mortality attributed to raptors was greater than other potential mortality sources (Table 4.1). My results are inconsistent with the findings of Sargeant et al. (1984) who concluded that red fox were the major predator of adult female pintails during the nesting season. Although Sargeant et al. (1984) did not use radiotelemetry to evaluate red fox predation rates on adult female ducks, they estimated that pintails had the greatest vulnerability index to red fox relative to other ducks and that red fox killed about 1 nesting female/km² in North Dakota. Similarly, Cowardin et al. (1985) reported that red foxes also were responsible for the greatest proportion of mortalities of radiomarked female mallards during the breeding season in North Dakota and suggested avian predation on their study area was of limited significance. Differences in predator communities, landscape features and configuration, and habitat types between my Saskatchewan study area and their North Dakota
study areas are likely explanations for the differences in the distribution of mortalities. Alternatively, differential habitat use by pintails and mallards may account for the observed difference in mortality agents for pintails in Saskatchewan and mallards in North Dakota (Cowardin et al. 1985).

Pintails frequently nest in sparse cover, including crop stubble (Milonski 1958, Keith 1961, Stoudt 1971, Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Chapter 2), and use small ephemeral wetlands in cropland for feeding (Smith 1970, Steward and Kantrud 1973), which may increase the risk of mortality due to avian predators because of minimal overhead concealment. Optimum foraging theory predicts that predators should forage in habitats where foraging efficiency is maximized, not necessarily, where prey densities are highest (Krebs 1973). Raptors may obtain the greatest net energy gain by hunting in crop stubble because of the lack of visual obscurity of prey species compared to habitats with greater overhead concealment. Negative relationships between vegetative ground cover and foraging time have been found for Swainson’s hawks (Bechard 1982), ferruginous hawks (Wakeley 1978), and red-tailed hawks (Baker and Brooks 1981). Although Preston (1990) failed to find a relationship between ground cover and foraging time for red-tailed hawks, he noted availability of perch sites also influenced foraging habitat use. Abandoned buildings, fence posts, shelterbelts, and snags were plentiful on my study area and frequently used as perch sites by these species.

From an evolutionary standpoint, use of open habitats with little concealment by pintails may be a strategy for females to reduce the risk of predation by mammalian predators. Females have a greater line of sight and increased opportunity to avoid mammalian predators approaching on foot. Habitats such as crop stubble for nesting or ephemeral or temporary
wetlands in cropland for feeding or loafing may mimic open habitats in which pintails evolved. The relatively recent expansion of agriculture and encroachment of aspen (*Populus tremuloides*) and willow (*Salix* spp.) in the mixed and short grass prairies (Maini 1960) may have altered the composition of the predator community by providing perch sites and nesting sites for raptors in a landscape where these resources were probably scarce. These recent anthropogenic habitat changes may increase the risk of predation on pintails by raptors because of abundant perch sites in the proximity of open habitats.

I attributed only 1 mortality to red fox depredation, but I may have underestimated red fox depredation as an important mortality agent. Red foxes typically capture nesting females (Sargeant et al. 1984), which were likely underrepresented in my study. Red foxes also tend to avoid wet areas (Sargeant et al. 1972) where non-nesting females were located. Furthermore, I observed 2 instances (1 pintail from this study and 1 mallard in a concurrent renesting study [Chapter 5]) where red foxes chewed on transmitters and antennas resulting in a decrease of signal strength. If this was a frequent behavior of red foxes and some transmitters became inoperative, I may have right censored some females that were killed by foxes. I also documented 1 mortality due to collision with overhead power lines. Although this type of mortality is prevalent in the prairies (Krapu 1974) and was documented for female pintails in Alberta (Guyn and Clark 2000) I believe collisions with power lines account for minor losses on my study area, but may be more problematic when power lines are adjacent to wetland complexes.

I was unable to assess the effect of nesting status (non-nesting days vs. days incubating an active nest) on survival because of few exposure days (413 days) and frequent gaps during the 75-day interval when females were incubating a clutch. However, 3 females
suffered mortalities (2 avian predator, 1 red fox) on days when females were incubating a known clutch. Further descriptive investigation revealed that female mortality might have been higher (0.73 mortalities/100 radio exposure days vs. 0.35 mortalities/100 radio exposure days) while females were incubating a clutch compared to non-nesting or laying periods, which is consistent with the findings of Kirby and Cowardin (1986). Furthermore, I was unable to examine effects of nest site habitat on female survival or cause-specific mortality. I suspect nesting habitat or microhabitat variables at the nest site could influence survival for incubating pintails.

**MANAGEMENT IMPLICATIONS**

Mortality of female pintails during the nesting season may be greater than winter mortality even when hunting is included as a mortality agent. My results are consistent with the conclusions of Miller et al. (1995) that if gains in annual survival are desired managers should examine the breeding period for opportunities to achieve increases. I identified raptors as the primary mortality agent for female pintails in southern Saskatchewan, likely due to their use of open habitats in close proximity to perch sites used by raptors. Management programs that provide nesting or wetland habitats with overhead concealment may decrease the risk of predation on pintail females by raptors.

I emphasize the importance of partitioning survival into segments of the annual cycle and specific periods within breeding season. I believe that further investigation into breeding season survival and cause-specific mortality for female pintails is warranted. Survival estimates are needed from other parts of the prairie pothole region and Alaska. Furthermore, information regarding survival during molt and spring and fall migration are crucial to
improve our understanding of waterfowl population regulation, develop accurate population models, and improve management decisions.

LITERATURE CITED


CHAPTER 5. INTERSPECIFIC COMPARISONS OF NORTHERN PINTAIL AND MALLARD RENESTING ECOLOGY

Waterfowl (*Anas* spp.) often suffer high rates of nest failure, largely due to predation. Low nest success has been viewed as the most important factor limiting waterfowl productivity (Cowardin et al. 1985, Johnson et al. 1992, Greenwood et al. 1995, Beauchamp et al. 1996). In the prairies, nest success estimates are often below the estimated 15% necessary for self-sustaining mallard (*A. platyrhynchos*) and northern pintail (*A. acuta*; hereafter – pintail) populations (Cowardin et al. 1985, Klett et al. 1988). Renesting, the laying of a replacement clutch following failure of a previous nesting attempt (Sowls 1955), is a common reproductive strategy that allows females to compensate for low nest success and to increase their seasonal reproductive success (Cowardin and Johnson 1979). Knowledge of renesting rates and factors that affect renesting propensity are important to accurately model waterfowl productivity and develop reliable life-cycle models (Johnson et al. 1987, Carlson et al. 1993, Flint et al. 1998).

Carlson et al. (1993) reported that the breeding ecologies of pintails and mallards were similar enough to justify using the nest initiation function from the mallard productivity model (Johnson et al. 1987) in the pintail productivity model to predict the estimated number of nest initiations per pair. An analysis of covariance (ANCOVA) revealed that neither the slopes nor intercepts differed for pintails or mallards when the predicted numbers of nesting attempts were regressed on wetland abundance (Carlson et al. 1993). However, their indices of nesting attempts for pintails and mallards were calculated by crudely examining relationships between search area, number of successful nests found, nest success estimates, and breeding pair counts from annual surveys at Woodworth, North Dakota, 1965-1981.

Advancements in radiotelemetry have since allowed researchers to estimate nesting intensity
by directly observing individuals, rather than relying on crude indices. Within the last decade, several researchers have used radiotelemetry to evaluate renesting propensity in pintails (Grand and Flint 1996a, Guyn and Clark 2000, Chapter 3) and mallards (Rotella et al. 1993, Paquette et al. 1997). Consequently, researchers have made interspecific comparisons of renesting rates and renest frequency and concluded that pintails have a lower propensity to renest than mallards (Austin and Miller 1995, Miller and Duncan 1999, Guyn and Clark 2000). I believe that such comparisons should be made with caution because pintail and mallard renesting rates and renesting frequency are variable depending on habitat conditions (Krapu et al. 1983, Cowardin et al. 1985, Chapter 3). Presently, all telemetry based interspecific comparisons of renesting rates of wild, free ranging ducks are based on data collected over different geographic regions and over different years, where environmental conditions such as climate, wetland abundance, and food availability differ. To my knowledge, no one has examined the renesting ecology of pintails and mallards with radiotelemetry controlling for such environmental variation to permit valid interspecific comparisons. Sowls (1955) made valid interspecific comparisons of renesting in pintails and mallards by resighting color-marked hens, but detection rates and emigration rates of color-marked hens were unknown. My objectives were to examine the influence of species (pintail, mallard), female age (second-year, after second-year), date of clutch loss, incubation stage at clutch loss, female body condition (body mass adjusted for structural size, date, of capture), and on renesting propensity and renest intervals, and to directly compare renesting ecology of pintails and mallards.
STUDY AREA

I conducted research from April to July during 2000 on a 16,576 ha (64 square-mile) area on the edge of the Missouri Coteau in south-central Saskatchewan (49°35’ N, 104°29’ W), centered about 10 km south and 40 km west of the town of Weyburn, SK. Topography ranged from gently rolling pastures in the southwest to relatively flat cropland in the northeast. Wetlands interspersed in these habitats ranged from small ephemeral basins (< 1 ha) to a large (approx 290 ha) semi-permanent basin. Approximately 13,095 ha (79%) were dominated by cereal grain and oil-seed agriculture, primarily spring wheat (*Triticum spp.*) and canola (*Brassica spp.*). During my study, 86% of the cropland was left over-winter in crop stubble; the remaining cropland was tilled in the fall leaving bare dirt. Other lands in the study area were pastures, hayfields, pond margins, road right-of-ways, odd areas (small areas of grass ≤ 2 ha found in cropland such as rock piles and fence rows), and 256 ha of nesting cover planted under the North American Waterfowl Management Plan (U.S. Fish and Wildlife Service [USFWS] et al. 1994). Wetland densities were 30% below the long-term average for this region in 2000 (USFWS 2000). This study site was selected because of consistently high pintail breeding pair densities determined from the Canadian Wildlife Service (CWS) May counts (USFWS 2000).

METHODS

Female Capture, Radiomarking, and Radiotelemetry

Nest searching was conducted on randomly assigned quarter sections starting in late April and ceasing in early July. Searching was conducted between 0800 and 1400 hrs when females were most likely to be present on incubation and laying stage nests (Gloutney et al. 1993). Waterfowl nests in grassland cover were located by systematically dragging a 70 m
chain between two ATVs (Higgins et al. 1977, Klett et al. 1986). Due to lower nest densities in stubble, sparser residual vegetation, and the large proportion of stubble on the study area, a 200 m cable was used to more efficiently search cropland. Nests and renests were marked with a 50 cm willow (*Salix* spp.) stick placed 1 m south and an individually numbered, 90 cm white lathe 20 m north of each nest. Global Positioning System (GPS) coordinates were also recorded for all pintail and mallard nests. I recorded species, clutch size, egg size, and developmental stage (Weller 1956) for each nest. I captured pintail and mallard females from randomly selected nests between 2 and 20 days of incubation throughout the nesting season using a modified Weller trap (Weller 1957) or a mist net. I measured culmen length (± 0.1 mm), left tarsus length (± 0.1 mm), left wing cord length (± 0.1 mm), and weighed (± 5 g) each female. I aged females as second-year (SY) or after second-year (ASY) using secondary covert feather markings (Gatti 1983b, Duncan 1985). Each female was fitted with a USFWS aluminum leg band and a 5 g prong and suture radio transmitter (< 1% of body mass, Advanced Telemetry Systems, Isanti, MN) described by Mauser and Jarvis (1991), but with a slightly modified attachment procedure (Peitz et al. 1995). Transmitters had mortality sensors and expected battery lives of 100 days. To minimize stress, each female was given a 0.2 ml subcutaneous injection of lidocane, a local anesthetic, at the attachment site prior to the procedure. Total handling time averaged 13.1 minutes from the time I removed a female from the trap or net, measured and fitted her with a radio transmitter, and released her near the nest site following the procedure. All procedures in this study were approved by Louisiana State University Institutional Animal Care and Use Protocol A98-3, and University of Saskatchewan Animal Care Committee 03622-AI on behalf on the Canadian Council of Animal Care.
To initiate renesting, I removed clutches 3 days after radio attachment. I suspected that this 3-day acclimation period minimized radio effects on renest likelihood or interval (T. Arnold, Institute for Waterfowl and Wetlands Research, personal communication). If a nest was depredated or the female abandoned her nest before the end of the acclimation period, I used the first date when she was radiolocated off the nest as the start of the renest interval. I tracked radio-marked females a minimum of once daily with truck-mounted, dual, 4-element Yagi antennas unless road conditions prohibited access through the study area. I located females between the hours of 0800 and 1400 hours until a female was triangulated to the same location in potential nesting cover for 3 consecutive days (Paquette et al. 1997). If a female was in potential nesting cover for 3 consecutive days, I approached the location on foot and attempted to flush the female and find the nest. If a female flushed at a long distance from nesting cover and the observer could not locate the nest, I used a dog to increase the probability of finding her renest. A renest was defined as \( \geq 1 \) egg in a new nest site (Sowls 1955). Renest initiation date was calculated by subtracting the sum of clutch size and incubation stage from the date the renest was located. Renest interval, the number of days between the date of the unsuccessful termination of the previous clutch and initiation date of a renest, was calculated for each female. Distance between nest sites was recorded with a 200 m distance tape if \( \leq 200 \) m or GPS if \( > 200 \) m. After renests were located I did not visit the nest again until the projected forth day of incubation, unless the radiolocation clearly indicated that the female was away from her nests. Females were allowed to lay a full replacement clutch, and their eggs were then taken on the fourth (\( \pm 1 \) day) day of incubation. Females were tracked until they could
no longer be located or moved to molting areas. Telemetry from fixed-wing aircraft was conducted every 12 - 14 days to locate females that could not be found from the ground (Gilmer et al. 1981).

**Statistical Analyses**

Body Size and Condition. - I conducted all statistical analyses using SAS statistical software (SAS Institute Inc. 1999). I indexed structural size for each species using principle components analysis (PROC PRINCOMP) of the correlation matrix of the 3 morphological measures taken from captured females. I used the first principle component (PC1) scores as a composite measure of structural size for each female (Alisauskas and Ankney 1987). I regressed (PROC GLM) female body mass on PC1 and used her residual from the regression as a measure of size adjusted body mass (Alisauskas and Ankney 1987). I used an analysis of covariance (ANCOVA) to examine the effects of species (pintail, mallard), female age (SY or ASY), incubation stage at capture (STAGE) and date of capture (DATE) on size-adjusted body mass. I used the residual for each female from the ANCOVA as a measure of species and date adjusted body mass (CONDITION). I used the adjusted body mass of each female as a measure of her condition in subsequent survival analyses (Dufour et al. 1993).

Renesting Propensity and Renest Intervals. - I used logistic regression (PROC LOGISTIC) to examine the effects of species (pintail, mallard), female condition, DATE, STAGE, and all 2-way interactions on the probability of a female renesting once. Females depredated before renesting or that were not consistently located following radio attachment were excluded from further renesting analysis. I used a forward-selection criterion to identify the best predictive logistic model. Variables were added to the model if they provided significant improvement (P ≤ 0.05) to the log likelihood.
I used an ANCOVA (PROC GLM) to assess the effects of species, female condition, DATE, and STAGE on renest interval. Renest interval was log-transformed to meet model assumptions of normality and homoscedasticity (Neter et al. 1996). I used a forward-selection criterion and variables were added to the model if they were significant at an alpha level of 0.05. I tested all 2-way interactions among significant variables. Phillips and Tienhoven (1962) reported that the ovaries and oviduct reached near maximum reduction in mass by 6 - 8 days incubation. Therefore, I used piecewise regression (Neter et al. 1996) to further examine if the relationship between renest interval and STAGE differed between early (≤ 8 days) and late incubation (> 8 days). I did not examine relationships for multiple renest attempts due to low sample size. I was unable to examine the effects of female age on renest propensity or renest interval due to a small sample size and quasi complete separation of sampling points in the logistic model.

Clutch Size. -- I used an ANCOVA to test effects of species and date of nest initiation on clutch size. I used the residuals from the ANCOVA as measures of species and date adjusted clutch size and used a paired $t$-test to compare differences in date adjusted clutch size between initial nests and renest of individual females. Nests were excluded from clutch size analyses if they were depredated before a full clutch was laid or exhibited evidence of a partial depredation. Means are reported ± standard error unless otherwise noted.

RESULTS

Body Size and Condition

Mean body mass at the time of capture was 676.1 ± 8.1 g for pintails (n = 41) and 925.9 ± 10.3 g for mallards (n = 40). For pintails, PC1 explained 48.6% of the variation among morphologic measurements, with factor loadings positive and ranging from 0.36
(tarsus length) to 0.70 (wing cord length). Pintail female body mass was positively related to
PC1 scores ($F_{1,39} = 12.85, P < 0.001, r^2 = 0.25$). Similarly, for mallards, PC1 explained
45.1% of the variation among morphologic measurements and all factor loadings were
positive and ranged from 0.49 (culmen length) to 0.66 (wing cord length). The regression of
mallard body mass on PC1 showed a positive relationship ($F_{1,38} = 7.08, P = 0.01, r^2 = 0.16$).
Size adjusted body mass decreased with date of capture ($F_{1,79} = 11.76, P < 0.001$, Fig. 5.1),
but was unrelated STAGE and similar between species ($P > 0.05$).

**Renesting Propensity and Renest Intervals**

Of the 41 pintails and 40 mallards I radio marked, 4 pintails were depredated before
renesting, and 3 pintails and 2 mallards either moved off the study area or had their radios fail
so they were excluded from renesting analyses. Overall renesting rates were 41.2% and
60.5% for pintails and mallards, respectively. Because clutches were taken throughout the
entire nesting season, it is possible that some females were already incubating a renest clutch
at the time of capture; therefore these renesting estimates are biased low. To minimize this
bias, I reanalyzed the data, but only included females likely to be incubating first nests by
limiting the sample to females with nest initiation dates prior to the earliest known renest
initiation date for each species (14 May - pintails, 17 May - mallards). Renesting rates for
likely first nesting females were 61.9% (n = 21) for pintails and 84.6% (n = 26) for mallards.
Of the females that renested, mallards initiated more multiple renests than pintails (Table
5.1.). My final model (Hosemer and Lemeshow Goodness-of-Fit Test, $\chi^2_{8} = 9.92, P = 0.271$)
indicated that renesting propensity was greater for mallards than pintails (Wald $\chi^2_{1} = 5.14, P <
0.05$) and was negatively associated with DATE (Wald $\chi^2_{1} = 17.61, P < 0.001$, Fig. 5.2).
Figure 5.1. Relationship between size adjusted body mass (condition) of female northern pintails and mallards and nest initiation date in southern Saskatchewan, 2000.
Table 5.1. Number of radio-marked female northern pintails and mallards and renesting rates in a highly agricultural landscape in southern Saskatchewan, 2000.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pintail</th>
<th>Mallard</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females Radioed</td>
<td>41</td>
<td>40</td>
</tr>
<tr>
<td>Depredated a</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Not Located b</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Renested</td>
<td>14 of 34</td>
<td>23 of 38</td>
</tr>
<tr>
<td>2 Renests c</td>
<td>8 of 14 d</td>
<td>12 of 22 e</td>
</tr>
<tr>
<td>3 Renests c</td>
<td>1 of 6</td>
<td>6 of 11 f</td>
</tr>
<tr>
<td>4 Renests c</td>
<td>0 of 1</td>
<td>4 of 6 g</td>
</tr>
</tbody>
</table>

a Females depredated before renesting and excluded from renesting analyses.
b Females that experienced radio failure or could not be located and were excluded from renesting analysis.
c Includes only females consistently monitored from previous renest.
d Contained 4 continuation nests, the laying of a replacement in new nest bowl without interruption to the laying sequence (Arnold and Rohwer, 1991).
e Contained 6 continuation nests.
f Contained 2 continuation nests.
g Contained 1 continuation nest.
Figure 5.2. Predicted probability of northern pintail and mallard females renesting given date of clutch loss in southern Saskatchewan, 2000.
Renesting propensity was unrelated to female condition, STAGE, or any 2-way interactions ($P > 0.05$).

Mean renest interval was similar for pintails (11.57 ± 0.96 days, range 8 – 20 days) and mallards (12.17 ± 1.40 days, range 7 - 36 days). The log of renest interval increased with STAGE ($F_{1,35} = 7.78 \ P < 0.01$, $r^2 = 0.18$, Fig. 5.3), but I found no evidence of separate slopes between early ($\leq 8$ days) and late ($> 8$ days) incubation ($P > 0.05$). Log of renest interval was unrelated to DATE or female condition ($P > 0.05$). For females that initiated multiple renests, mean renest intervals for females that lost their clutch during laying (pintails - 3.33 ± 1.50 day, n = 6; mallards - 3.65 ± 0.85 day, n = 17) was lower than females that lost their clutch during incubation (pintails - 9.33 ± 0.88 day, n = 3; mallards - 8.00 ± 0.77 day, n = 5). Mean distances between nest sites were similar for pintails (408 ± 169 m, range 14 to 2490 m) and mallards (642 ± 187 m, range 16 – 3220 m, Fig. 5.4).

**Clutch Size**

Mean mallard clutch size (8.85 ± 0.19 eggs, n = 48) was significantly higher than mean pintail clutch size (7.40 ± 0.17 eggs, n = 45; $\beta = 1.46$, SE = 0.21, $P < 0.001$). Clutch size was highly negatively correlated with nest initiation date ($\beta = -0.06$, SE = 0.01, $P < 0.001$), but declined with nest initiation date at similar rates for both species. For a sample of 4 pintails and 7 mallards that had a known initial clutch size and completed a renest clutch, clutch sizes adjusted for laying date were similar between initial nests and renests of for both pintails ($\Delta \bar{x} = -2.4 \pm 1.59$ eggs, $t_3 = 2.86$, $P = 0.07$) and mallards ($\Delta \bar{x} = -0.88 \pm 1.20$ eggs, $t_6 = 0.63$, $P = 0.55$).
Figure 5.3. Relationship between renest interval and incubation stage at clutch loss for female northern pintails and mallards in southern Saskatchewan, 2000.

\[ \ln(Y) = 2.01 + 0.05(\text{STAGE}) \]
Figure 5.4. Distance between nesting attempts for female northern pintails and mallards in southern Saskatchewan, 2000.
DISCUSSION

My telemetry based estimates of renesting rates for nest-trapped pintail and mallard females likely incubating a first clutch were similar to other recent telemetry based renesting estimates (Table 5.2). From an evolutionary standpoint, one advantage of early nesting is increased opportunity to renest (Rohwer 1992). Therefore, species like pintails and mallards should both be persistent renesters. However, my data suggest that pintails have a lower propensity to renest than mallards.

I offer 2 potential hypotheses for lower renesting propensity of pintails relative to mallards. First, differential wetland selection by breeding pintails and mallards within the same landscape may affect the availability of food to each species. I observed pintails on ephemeral and temporary ponds at a greater frequency than mallards (Richkus and Rohwer, unpublished data). Similarly, pintails used shallow or ephemeral wetlands for feeding (Smith 1970) and pintails occurred more frequently on temporary and seasonal cropland ponds with a tilled bottom than mallards (Stewart and Kantrud 1973). Compared to non-tilled wetlands, tilled wetlands generally contain fewer aquatic invertebrates, the primary food of laying pintails (Krapu 1974). In addition, ephemeral and temporary ponds are the first to dry as the season progresses, which may limit access to foods for pintails earlier than mallards using deeper, more permanent ponds.

A second hypothesis for lower renesting affinity of pintails relative to mallards is that pintails may make a greater investment in future reproductive potential (i.e. survival) than mallards at a cost to current reproductive effort (i.e. clutch size and renest frequency). Although Arnold (1987) found little evidence of survival – fecundity tradeoffs among precocial game birds, he reported that body mass was negatively correlated with clutch size.
Table 5.2. Percentage of wild free ranging females that renested at least once and maximum number of renests per female of northern pintails and mallards in recent radio telemetry studies using abdominal implant, anchor/suture, and sutured backpack transmitters.

<table>
<thead>
<tr>
<th>Species/Location</th>
<th>Rate (%)</th>
<th>Frequency</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Northern pintail</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alaska (^a)</td>
<td>56</td>
<td>2</td>
<td>Grand and Flint 1996(^a)</td>
</tr>
<tr>
<td>Alberta (^a)</td>
<td>85</td>
<td>2</td>
<td>Guyn and Clark 2000</td>
</tr>
<tr>
<td>Alberta (^b)</td>
<td>55</td>
<td>2</td>
<td>Guyn and Clark 2000</td>
</tr>
<tr>
<td>Saskatchewan (^a)</td>
<td>61 - 90</td>
<td>3</td>
<td>Chapter 3</td>
</tr>
<tr>
<td><strong>Mallard</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alberta (^a)</td>
<td>60-81</td>
<td>5</td>
<td>Rotella et al. 1993</td>
</tr>
<tr>
<td>Parkland Canada (^a)</td>
<td>--</td>
<td>1.1-2.9 (^c)</td>
<td>Paquette et al. 1997</td>
</tr>
</tbody>
</table>

\(^a\) Nest-trapped females likely incubating first clutches.
\(^b\) Pre-laying females.
\(^c\) Means number of nests per female.
It is interesting to note that pintails have a smaller body mass, yet have a smaller clutch size relative to mallards, which may indicate that pintails make a smaller investment in current reproductive effort. Regardless of the mechanism, lower renesting by pintails reduces hen success, the proportion of hens that hatch 1 or more eggs, and may partially explain the recent lower pintail productivity relative to mallards.

Not surprisingly, I found a strong seasonal decline in renesting propensity for both pintails and mallards. Similar relationships were found for sub-arctic nesting pintails on the Yukon Kuskokwim Delta, Alaska (Grand and Flint 1996a) and prairie nesting pintails in Alberta (Guyn and Clark 2000) and Saskatchewan (Chapter 3) as well as prairie nesting mallards (Krapu et al. 1983, Cowardin et al. 1985). This effect was likely associated with the seasonal variation in water levels, which influences availability of foods to breeding females. Ultimately, late renesting results in later hatch dates, which are associated with lower brood and duckling survival (Grand and Flint 1996b, Guyn and Clark 1999).

I failed to detect a significant relationship between renesting propensity and female condition or incubation stage at the time of clutch loss. However, I found a decline in female condition with later nest initiation dates and the rate of decline was similar between species. Similar relationships were found for pintails on the Y-K Delta (Grand and Flint 1996a) and Saskatchewan (Chapter 3). I suspect the seasonal decline in female condition likely implies that females in better condition nest earlier to maximize recruitment potential (Rohwer 1992). Interestingly, I did not find a significant negative relationship between female condition and incubation stage at capture for pintails or mallards, which is common for most waterfowl due to the energetic cost of incubation (Harris 1970, Gatti 1983a, Afton and Paulus 1992).
My mean renest interval estimates for pintails and mallards were similar and increased with incubation stage at clutch loss at similar rates for each species. Similar relationships have been found for pintails (Chapter 3) and mallards (Sowls 1955, Swanson et al. 1986), likely due to regression of the ovaries during incubation. Phillips and Tienhoven (1962) reported that the ovary and oviduct reached near maximum reduction in mass by 6 – 8 days incubation, however I found no evidence of differing rates of increase of renest interval with stage between early (≤ 8 days) and late incubation (>8 days). I suspect this lack of a change in slope between early and late incubation implies that other physiological factors, which were not reflected in my metric of female condition, possibly affected renest intervals. I found no relationship between female condition and renest interval, which was consistent with Krapu’s (1974, 1981) findings that renesting ducks typically have few endogenous nutrient reserves and do not use reserves for renest clutch production (Esler and Grand 1994). However, ducks may need to have some threshold of stored reserves before renesting, possibly to overcome the energetic cost of incubation (Gatti 1983a, Afton and Paulus 1992).

Seasonal declines in clutch size have been reported in almost all waterfowl (see Rohwer 1992) and many researchers have hypothesized that the decline in part is due to smaller clutches laid by renesters. Although mean clutch size was smaller for pintails than mallards, similar rates of seasonal decline suggest the same factors may govern this trend for both species. Although renest clutches were smaller than initial clutches for each species, after correcting for nest initiation date, clutch size was similar between initial nests and renests. Similar relationships were found for captive-reared pintails (Duncan 1987) and captive-reared mallards (Batt and Prince 1979), suggesting that date and not renesting was responsible for seasonal declines in clutch size.
My results strongly support previous suppositions that pintails are less persistent renesters than mallards (Miller and Duncan 1999, Guyn and Clark 2000) and may in part explain the lack of response of pintails to improved wetland habitat conditions on the prairies during the late 1990s (USFWS 2000). Although most pintails renest, few renest multiple times, whereas mallards are more persistent renesters. I suggest that differential wetland habitat selection by pintails and mallards may partially explain this trend and examination of the importance of sheet water and temporary ponds to breeding pintails warrant further investigation. Furthermore, existing life cycle and production models should be expanded upon so these tools can be used to reliably evaluate management actions.

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____. 1981. The role of nutrient reserves in mallard reproduction. Auk 91:278-290


CHAPTER 6. INTERSPECIFIC COMPARISONS OF FEMALE NORTHERN PINTAIL AND MALLARD SURVIVAL AND CAUSE-SPECIFIC MORTALITY

Interspecific comparisons of survival are important for developing or testing hypotheses regarding evolutionary life history strategies and developing species-specific management programs (Johnson et al. 1992). Estimates of annual survival rates for most waterfowl (Anas spp.) are obtained from models (Brownie et al. 1985) using direct band recoveries. Although annual survival estimates for pintails (A. acuta) tend to be greater relative to mallards (A. platyrhynchos; Anderson 1975, Bellrose 1980, Reinecker 1987, Hestbeck 1983, Nichols and Hines 1987), these estimates may not be directly comparable because they fail to control for spatial and temporal variation where weather, habitat conditions, risk of predation, and hunting intensity may differ. Furthermore, annual survival estimates derived from banding do not allow survival to be partitioned into segments of the annual cycle or identify cause-specific sources of natural mortality, which may differ between species.

In contrast, advancements in radiotelemetry have allowed researchers to estimate survival and cause-specific sources of natural mortality by directly monitoring individuals during particular segments of the annual cycle. Such studies are crucial to improve our understanding of waterfowl population regulation, develop accurate population models, and improve management decisions (Johnson et al. 1992). Within the last 15 years, several studies have used radiotelemetry to assess winter survival of female pintails (Migoya and Baldassarre 1995, Miller et al. 1995, Cox et al. 1998) and mallards (Reinecke et al. 1987, Bergan and Smith 1993, Dugger et al. 1994). With the exception of southwest Louisiana (Cox et al. 1998), female pintails generally had greater winter survival rates than mallards. However, in Chapter 4, I speculated that female pintails in southern Saskatchewan had a
lower telemetry-based survival estimate than female mallards during the breeding season in North Dakota (Cowardin et al. 1985) and Minnesota (Kirby and Cowardin 1986).

Again, such interspecific comparisons of telemetry-based survival estimates are not strictly comparable because data were collected over different geographic regions and different years where habitat conditions, land use patterns, and composition of the predator community may differ. To my knowledge, nobody has examined the breeding season survival of pintails and mallards controlling for such variation to permit valid interspecific comparisons. My primary objectives were to estimate and directly compare survival estimates and cause-specific mortality rates of female pintails and mallards during the nesting season where a large fraction of annual mortality occurs (Johnson et al. 1992). I tested for variation in survival in relation to species (pintail, mallard), female age (second-year, after second-year), and body condition at the time of capture.

**STUDY AREA**

I conducted research from April to July during 2000 on a 16,576 ha (64 square-mile) block on the edge of the Missouri Coteau in south-central Saskatchewan (49°35’ N, 104°29’ W), centered about 10 km south and 40 km west of the town of Weyburn, SK. Topography ranged from gently rolling pastures in the southwest to relatively flat cropland in the northeast. Wetlands interspersed in these habitats ranged from small ephemeral basins (< 1 ha) to a large (approx 290 ha) semi-permanent basin. Approximately 13,095 ha (79%) were dominated by cereal grain and oil-seed agriculture, primarily spring wheat (Triticum spp.) and canola (Brassica spp.). During my study, 86% of the cropland was left over-winter in crop stubble; the remaining cropland was tilled in the fall leaving bare dirt. Other lands in the study area were pastures, hayfields, pond margins, road right-of-ways, odd areas (small areas
of grass ≤ 2 ha found in cropland such as rock piles and fence rows), and 256 ha of nesting
cover planted under the North American Waterfowl Management Plan (U.S. Fish and Wildlife
Service [USFWS] et al. 1994). Wetland densities were 30% below the long-term average for
this region in 2000 (USFWS 2000). This study site was selected because of consistently high
pintail breeding pair densities determined from the Canadian Wildlife Service (CWS) May
counts (USFWS 2000). Potential predators of pintail and mallard females included: coyote
(*Canis latrans*), red fox, mink (*Mustela vison*), northern harrier (*Circus cyaneus*), red-tailed
hawk (*Buteo jamaicensis*), Swainson’s hawk (*B. swainsoni*), ferruginous hawk (*B. regalis*)
and great horned owl (*Bubo virginianus*).

**METHODS**

**Female Capture, Radiomarking, and Radiotelemetry**

I captured pintail and mallard females from randomly selected nests between 2 and 20
days of incubation (Weller 1956) from April to June using a modified Weller trap (Weller
1957) or a mist net. I measured culmen length (± 0.1 mm), left tarsus length (± 0.1 mm), left
wing cord length (± 0.1 mm), and weighed (± 5 g) each female. I aged females as second-
year (SY) or after second-year (ASY) using secondary covert feather markings (Gatti 1983,
Duncan 1985). Each female was fitted with a USFWS aluminum leg band and a 5 g prong
and suture radio transmitter (< 1% of body mass, Advanced Telemetry Systems, Isanti,
Minnesota, USA), described by Mauser and Jarvis (1991), but using a slightly modified
attachment procedure (Peitz et al. 1995). Transmitters had mortality sensors and expected
battery lives of 100 days. To minimize stress, each female was given a 0.2 ml subcutaneous
injection of lidocane, a local anesthetic, at the attachment site prior to the procedure. Total
handling time averaged 13.1 minutes from the time I removed a female from the trap or net,
measured and fitted her with a radio transmitter, and released her near the nest site following
the procedure. All procedures in this study were approved by Louisiana State University
Institutional Animal Care and Use Protocol (A98-3), and University of Saskatchewan on
behalf on the Canadian Council of Animal Care (03622-AI).

I monitored survival during an induced renesting study (Chapter 5), in which clutches
were removed 3 days after transmitter attachment to initiate renesting. I tracked radio-marked
females a minimum of once daily using truck-mounted, dual, 4-element Yagi antennas unless
road conditions prohibited access through the study area. I located females between the hours
of 0800 and 1400 hours (Gloutney et al. 1993) until they were triangulated to the same
location in potential nesting cover for 3 consecutive days (Paquette et al. 1997). If a female
was in potential nesting cover for 3 consecutive days, I approached the location on foot and
attempted to flush the female and find the nest. If a female was located in crop stubble
scheduled to be cultivated within a few days, I approached the location immediately to avoid
missing a renesting attempt. After renests were located I did not visit the nest again until the
projected fourth day of incubation to remove the clutch, unless the radiolocation clearly
indicated that the female was away from her nest. I tracked and assessed status (alive or
dead) of females until they could no longer be located or moved to molting areas. I
immediately retrieved carcasses and transmitters with activated mortality sensors and
identified cause of death from physical evidence at the recovery site (Einarsen 1956, Sargeant
et al. 1998) and appearance of the transmitter. Causes of female mortalities were classified as
avian, red fox, collision with power line, or unknown. Telemetry from fixed-wing aircraft
was conducted every 12 - 14 days to locate females that could not be found from the ground
(Gilmer et al. 1981).
Statistical Analyses

Body Size and Condition. - I conducted all statistical analyses using SAS statistical software (SAS Institute Inc. 1999). I indexed structural size for each species using principal components analysis (PROC PRINCOMP) of the correlation matrix of the 3 morphological measures taken from captured females. I used the first principal component (PC1) scores as a composite measure of structural size for each female (Alisauskas and Ankney 1987). I regressed (PROC GLM) female body mass on PC1 and used her residual from the regression as a measure of size adjusted body mass (Alisauskas and Ankney 1987). I used an analysis of covariance (ANCOVA) to examine the effects of species (pintail, mallard), female age (SY or ASY), incubation stage at capture and date of capture on size-adjusted body mass. I used the residual for each female from the ANCOVA as a measure of species and date adjusted body mass (CONDITION). I used the adjusted body mass of each female as a measure of her condition in subsequent survival analyses (Dufour et al. 1993).

Survival and Cause Specific Mortality. - I used Cox (1972) proportional hazards regression generalized for staggered entry (PROC PHREG; Allison 1995) to test for differences in survival (considering all forms mortality) relative to species (pintail, mallard), female age (SY or ASY), female condition at capture, and all 2-way interactions. I observed no mortalities within 7 days of release; therefore, I assumed stress from capture and handling had no effect on survival (Pollock et al. 1989) and females were entered into the model the day following release. I used 6 May as the origin and right-censored females if they were alive on 14 July when the radio tracking ended. This interval was fully represented for both pintail and mallards. Females with radiotransmitter failure or that emigrated from the study area were right censored the last day of observation. I assumed that right censorship was
random and independent of fate of radiomarked females (Pollock et al. 1989). Furthermore, I assumed survival was independent among all females and that radiotransmitters had no effect on survival (Pollock et al. 1989). I also assumed that left censored individuals, due to staggered entry, had survival distributions similar to previously marked birds (Pollock et al. 1989). To arrive at my final model, I used backward selection and removed non-significant ($P > 0.05$) terms from the model beginning with the highest order interactions. I used the product-limit method (Kaplan and Meier 1958) generalized for staggered entry to calculate periodic survival rates (Allison 1995).

Cause-specific mortality was defined as the probability of a female dying from a given mortality agent. I estimated cause-specific mortality rates for each of the 4 mortality agents as if they were the only source of mortality. For each model, I treated mortalities from competing mortality agents as right censored the day of death. For these estimates of cause-specific mortality, I assumed causes of mortality were independent. I did not perform tests for effects of species and female age on cause-specific mortalities rates because no clear standard exists by which to estimate variances for mortality rates of 0.0 (4 of 8 species-mortality agent combinations), particularly with a staggered entry design (Davis et al. 2001). Means are reported ± standard error unless otherwise noted.

**RESULTS**

**Body Size and Condition**

Mean body mass at the time of capture was 676.1 ± 8.1 g for pintails (n = 41) and 925.9 ± 10.3 g for mallards (n = 40). For pintails, PC1 explained 48.6% of the variation among morphologic measurements, with factor loadings positive and ranging from 0.36 (tarsus length) to 0.70 (wing cord length). Pintail female body mass was positively related to
PC1 scores \( F_{1,39} = 12.85, P < 0.001, r^2 = 0.25 \). Similarly, for mallards, PC1 explained 45.1\% of the variation among morphologic measurements and all factor loadings were positive and ranged from 0.49 (culmen length) to 0.66 (wing cord length). The regression of mallard body mass on PC1 showed a positive relationship \( F_{1,38} = 7.08, P = 0.01, r^2 = 0.16 \). Size adjusted body mass decreased with date of capture \( F_{1,79} = 11.76, P < 0.001, \) Fig. 6.1, but was unrelated stage and similar between species \( P > 0.05 \).

**Seasonal Survival and Cause-Specific Mortality**

I used fates of 41 pintail and 40 mallard females with 1012 and 1522 exposure days to estimate survival and cause-specific mortality from 6 May to 14 July. The overall survival rate for the 69 day period was \( 0.83 \pm 0.08 \) for pintails and \( 0.93 \pm 0.05 \) for mallards (Fig. 6.2). I found no evidence that the hazard function varied between species, ages, female condition at capture, or any 2-way interactions \( P > 0.37 \). I documented 4 pintail mortalities and determined that 2 were depredated by avian predators, 1 was killed by a collision with a power line, and 1 was killed by an unknown cause (Table 6.1). I documented 2 mallard mortalities and attributed both to depredation by red foxes (Table 6.1). Cause-specific mortality rates were highest due to raptors \( (0.08 \pm 0.05) \) and red foxes \( (0.07 \pm 0.05) \) for pintails and mallards, respectively (Table 6.1).

**DISCUSSION**

My 69 day, telemetry based survival estimate for female pintails during the nesting season was similar to estimates for female pintails from the same study area in 1998 and 1999 (Chapter 4). My female mallard survival estimate was slightly higher than estimates for mallards in North Dakota and Minnesota (Table 6.2). However, my 69-day interval was shorter than intervals for mallards in other studies (Table 6.2) suggesting that mallard survival
Figure 6.1. Relationship between size adjusted body mass (condition) of female northern pintails and mallards and nest initiation date in southern Saskatchewan, 2000.

\[ Y = 57.52 - 1.49(\text{Nest Initiation Date}) \]
Figure 6.2. Survival rate (6 May – 14 July, 69 days) of radiomarked female northern pintails (squares) and mallards (circles) in southern Saskatchewan, 1998-2000, considering all sources of mortality. Dashed lines (northern pintails) and dotted lines (mallards) denote 95% confidence intervals.
Table 6.1. Interval (6 May – 14 July, 69-day) mortality rates (M) for female northern pintails (n = 41) and mallards (n = 40) in southern Saskatchewan, 1998-2000.

<table>
<thead>
<tr>
<th>Mortality Agent</th>
<th>Pintails</th>
<th></th>
<th>Mallards</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mortalities</td>
<td>M</td>
<td>SE&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Mortalities</td>
</tr>
<tr>
<td>Avian predator</td>
<td>2</td>
<td>0.08</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>Red fox</td>
<td>0</td>
<td>0.00</td>
<td>---</td>
<td>2</td>
</tr>
<tr>
<td>Collision with power line</td>
<td>1</td>
<td>0.04</td>
<td>0.04</td>
<td>0</td>
</tr>
<tr>
<td>Unknown causes</td>
<td>1</td>
<td>0.05</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>4</td>
<td>0.17</td>
<td>0.08</td>
<td>2</td>
</tr>
</tbody>
</table>

<sup>a</sup> Standard errors were not computed when M = 0.00.
Table 6.2. Survival rates (S ± SE) of female pintails and mallards during the breeding season from radiotelemetry studies.

<table>
<thead>
<tr>
<th>Species</th>
<th>Region</th>
<th>Days</th>
<th>Age(^a)</th>
<th>S</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Pintail</td>
<td>Saskatchewan</td>
<td>69</td>
<td>SY, ASY</td>
<td>0.83 ± 0.08</td>
<td>This study</td>
</tr>
<tr>
<td>Northern Pintail</td>
<td>Saskatchewan</td>
<td>75</td>
<td>SY, ASY</td>
<td>0.81 ± 0.05</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>Mallard</td>
<td>Saskatchewan</td>
<td>69</td>
<td>SY, ASY</td>
<td>0.93 ± 0.05</td>
<td>This study</td>
</tr>
<tr>
<td>Mallard</td>
<td>North Dakota</td>
<td>153</td>
<td>SY, ASY</td>
<td>0.81</td>
<td>Cowardin et al. 1985</td>
</tr>
<tr>
<td>Mallard</td>
<td>Minnesota</td>
<td>169</td>
<td>AHY</td>
<td>0.71 ± 0.08(^b)</td>
<td>Kirby and Cowardin 1986</td>
</tr>
</tbody>
</table>

\(^a\) HY = hatch-year, AHY = after hatch-year, SY = second-year, ASY = after second-year.

\(^b\) Standard error misreported as 0.77 in Kirby and Cowardin 1986.
in my study was likely similar to estimates from North Dakota and Minnesota. In addition, I suspect that my estimate of survival during the nesting season is biased high because I monitored female survival during a concurrent study of induced renesting (Chapter 5). Days when radiomarked females were incubating a clutch were likely underrepresented relative to the population because clutches of radiomarked females were repeatedly removed in early incubation to assess pintail and mallard renesting propensity. Kirby and Cowardin (1986) reported that survival of female mallards during incubation was lower than other periods during the nesting season, confirming previous speculation that females suffer higher rates of mortality while attending nests (Johnson and Sargeant 1977, Sargeant et al 1984, Cowardin et al. 1985).

Although the nesting season survival of female pintails and mallards were not statistically different, my results suggest that pintails may have lower nesting season survival than mallards controlling for landscape level spatial and temporal variation. Furthermore, my results suggest that cause specific-mortality rates may differ between species (Table 6.1). Predation by raptors was the major cause of mortality for pintails, while predation by red foxes was the only cause of mortality for mallards. Sargeant et al. (1984) concluded that red fox were the major predator of both female pintails and mallards during the nesting season and reported that pintails and mallards had the 2 greatest vulnerability indices to red fox of dabbling ducks in North Dakota. Similarly, Cowardin et al. (1985) reported that red fox were also responsible for the greatest proportion of mortalities of radiomarked female mallards during the breeding season in North Dakota. However, my results suggest that on my study area, red fox predation of pintail females is less prevalent (Chapter 4).
I offer 2 potential hypotheses for the potential differences in survival estimates and cause-specific mortality rates between pintails and mallards. First, differential habitat use by breeding pintails and mallards within the same landscape may affect their vulnerability to different predators. Pintails may be at greater risk to predation by raptors because of their strong propensity to nest in sparse cover, including crop stubble with little overhead concealment (Milonski 1958, Keith 1961, Stoudt 1971, Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Chapter 2). In addition, pintails used shallow or ephemeral wetlands for feeding (Smith 1970) and pintails occurred more frequently on temporary and seasonal cropland ponds with a tilled bottom than mallards (Stewart and Kantrud 1973). On my study area, ephemeral wetlands in cropland had almost no emergent vegetation or residual cover for concealment from avian predators. Raptors frequently forage in open habitats such as crop stubble and negative relationships between vegetative ground cover and foraging time have been found for Swainson’s hawks (Bechard 1982), ferruginous hawks (Wakely 1978), and red-tailed hawks (Baker and Brooks 1981). I hypothesize that use of open habitats by pintails may increase their risk of predation by raptors, but may decrease their risk of predation by mammalian predators because females have a greater line of sight and increased opportunity to avoid approaching mammalian predators. Conversely, mallards frequently nest in habitats with dense cover with greater overhead concealment (Cowardin et al. 1985, Greenwood et al. 1995, Chapter 2), which may reduce risk of predation by avian predators, but increase their risk of predation by red fox.

Second, in chapter 5, I reported that mallards renested more frequently and later into the nesting season than pintails. Increased renesting likely increases the risk of predation by red fox, because they typically capture females at the nest (Sargeant et al. 1984) and tend to
avoid wet areas (Sargeant et al. 1972) where non-nesting females were located. For this reason, I may have underestimated red fox depredation as an important mortality agent for both species because days when females were incubating a clutch were likely underrepresented in my study relative to the population.

I failed to detect a difference in survival between SY and ASY females for pintails or mallards. Swanson et al. (1986) reported ASY female mallards had a greater renesting propensity relative to SY females. Therefore, I would predict that ASY females might experience greater breeding season mortality than SY females because of more potential exposure days incubating a clutch when risk of predation is higher (Kirby and Cowardin 1986). However, I failed to detect an age-specific difference in renesting propensity for these radiomarked females potentially explaining the lack of an age effect on female survival (Chapter 5) Conversely, one could predict ASY females may have greater survival than SY females due to previous encounters with and more experience eluding predators. However, my results suggest that females do not “learn” from previous encounters with predators, perhaps because their first encounter results in mortality.

Similar to previous studies on wintering female pintails (Migoya and Baldassarre 1995, Miller et al. 1995, Cox et al. 1998) and mallards (Reinecke et al. 1987, Dugger et al. 1994), I found no effect of body condition on survival during the breeding season. My sample consisted of randomly captured nesting females, but these females may have had a high measure of body condition relative to females that had not initiated a nest. In addition, Cox et al. (1998) speculated that one reason for their failure to detect any effect of condition on winter survival is that females in the poorest condition never arrived on the wintering grounds because of mortality during fall migration. Likewise, females in the poorest
condition may never arrive on the breeding grounds because of mortality during spring migration. Alternatively, food availability on the breeding areas may allow females to maintain a body condition above any possible survival threshold.

I was unable to assess the effect of nesting status (non-nesting days vs. days incubating an active nest) on survival because of few exposure days and frequent gaps during the 69-day interval when females were incubating a clutch. I also were unable to test the effects of nesting habitat on female survival. I suspect that these variables likely influence female survival while nesting and deserve further investigation. I identified avian predation as the primary mortality agent for female pintails in southern Saskatchewan, likely due to their use of open habitats for nesting, feeding, and loafing. Management programs that provide nesting habitat with overhead concealment may decrease the risk of avian predation on female pintails. For mallards, my results are consistent with the findings of Sargeant et al. (1984) and Cowardin et al. (1985) that red fox are a major predator of females during the nesting season. Although not statistically significant, female pintails had lower survival than mallards during the nesting season, which may in part explain the lack of response of pintails to improved wetland habitat conditions on the prairies during the late 1990s (USFWS 2000).

LITERATURE CITED


CHAPTER 7. CONCLUSION

My results strongly support previous speculation that on a landscape level, crop stubble may act as an ecological trap for prairie nesting pintails (Miller and Duncan 1999). The elimination of fall tillage on the prairies has created an abundance of crop stubble habitat. Unfortunately, this crop stubble serves as an ecological trap, which appears to be especially detrimental and largely unique to nesting pintails. Most (51%) pintail nests were found in crop stubble and generally pintails nested in habitats in proportion to their availability on the landscape. In contrast, most (82%) mallard nests were located in edge and grassland habitats, and they nested in habitats with dense cover in greater proportion to their availability and avoided crop stubble. My initial prediction based on the ecological trap hypothesis was that most nests would be destroyed by farm machinery during spring cultivation. However, that prediction was clearly wrong, as only 20-33% of nests in crop stubble failed due to spring cultivation. Nest success estimates in crop stubble on my study area were abysmal largely due to high rates of nest predation, not spring cultivation.

From an evolutionary standpoint, one advantage of early nesting is an increased opportunity to renest (Rohwer 1992). Therefore, one would predict that early nesting species like pintails would be persistent renesters. Although most (58%) pintails renested, my results suggest that most females renest only once and few initiate multiple renests. Furthermore, my results support previous suppositions that pintails are less persistent renesters than mallards. Annual and seasonal variation in pintail renesting propensity appears to be related to wetland abundance, which may affect food availability to breeding females (Krapu et al. 1983).

Nesting season survival for female pintails may be lower than winter survival even when hunting is included as a mortality agent. In addition, female pintails may have lower
nesting season survival than sympatric nesting female mallards. I identified raptors as the primary mortality agent for female pintails, whereas red foxes were the major predator of mallards. Pintail use of open habitats with little overhead concealment, such as crop stubble for nesting and ephemeral ponds in cropland for feeding and loafing (Stewart and Kantrud 1973), may explain their lower survival and greater risk of predation by raptors relative to mallards.

The pintail’s high propensity to nest in crop stubble where nest success is low, coupled lower renesting breeding season survival than mallards may partially explain the persistently low pintail population levels and meager response to improved wetland conditions during the mid to late 1990’s. I strongly agree with the recommendations of Miller and Duncan (1999) that management programs to facilitate pintail recovery should primarily be targeted at increasing nest success by providing “safe” nesting habitat.

Although this study provided answers to several critical questions concerning pintail breeding ecology, several questions remain unanswered. Most namely, why do pintails select nest sites with such sparse cover? Pintails selected sparser nest sites than mallards within similar habitat types, which indicated that pintails were clearly making a different choice. I hypothesized that the use of open habitats with little concealment may have been a strategy for females to reduce the risk of predation by mammalian predators. Females have a greater line of site and increased opportunity to avoid approaching mammalian predators. I found only 1 of 15 pintail mortalities was attributed to mammalian predators, compared to 2 of 2 mallard mortalities (Chapters 4, 6). Conversely, my results suggest that use of open habitats by pintails may increase the risk of predation by raptors (Chapters 4, 6), but this may be due to recent anthropogenic habitat changes that may have altered the composition of the predator
community such that avian predators are relatively more important predators of pintails in Saskatchewan than during the evolutionary past (see Chapter 4).

Ultimately, females should choose nest sites or adopt reproductive strategies that maximize their lifetime reproductive output (Rohwer 1992, Martin 1993). Nests in open habitats may be at a greater risk of failure (Hines and Mitchell, 1983, Crabtree et al. 1989, Clark and Shutler 1999), but if pintail females incurred a survival benefit, their choice to nest in sparse cover may reflect differing life history strategies. Pintails may make a greater investment in future reproductive potential (i.e. survival) than mallards at a cost to current reproductive effort (nest success, renesting frequency). However, data to examine lifetime survival with any confidence are largely lacking.

Although I found that on a landscape level, pintails general nest in habitats in proportion to their availability on the landscape, consideration also must be given to the implications of spatial scale in habitat selection studies (Johnson 1980). Given the hierarchical nature of habitat selection (Johnson 1980), my estimates of nesting habitat preference for pintails are likely biased because I selected a highly agricultural landscape within the Prairie Pothole Region (PPR) to examine nest site selection. The females I encountered in my study had previously selected southern Saskatchewan over other breeding areas in the PPR or Alaska. Within southern Saskatchewan, these females had previously selected to settle in a highly agricultural landscape over landscapes with greater proportion of grassland habitats. Studies in which pintails are marked before arrival on the breeding grounds and that examine pintail nest site selection on multiple spatial scales are critical to improve our understanding of pintail habitat site selection.
LITERATURE CITED


VITA

Kenneth Daniel Richkus, son of Richard and Vanessa Richkus was born 20 April 1974, in Baltimore, Maryland. He primarily grew up in Sterling, Virginia, and spent much of his free time during his youth hunting, fishing, training beagles, and enjoying the outdoors with his grandfather, Edmund Ward. He attended and graduated from the Thomas Jefferson High School for Science and Technology in Alexandria, Virginia in, 1992, where he developed a strong interest in science. In 1996, he graduated Summa Cum Laude as a Commonwealth Scholar from Virginia Polytechnic Institute and State University (Virginia Tech) in Blacksburg, Virginia, and received bachelor of science degrees in biology, and fisheries and wildlife science (wildlife science concentration). Upon graduation, he immediately began working as a research technician for the Department of Fisheries and Wildlife Science at Virginia Tech, which further spurred his interest in waterfowl and research. In 1997, he began working as a field assistant for the Delta Waterfowl and Wetlands Research Station where he met Dr. Frank Rohwer, who became his major professor later that year. Ken is presently a candidate for the degree of Doctor of Philosophy in wildlife and fisheries science at Louisiana State University’s School of Renewable Natural Resources.