

**NESTING AND DUCKLING  
ECOLOGY OF  
WHITE-WINGED SCOTERS  
(*MELANITTA FUSCA DEGLANDI*)  
AT REDBERRY LAKE,  
SASKATCHEWAN**

A Thesis

Submitted to the College of Graduate Studies and Research  
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Master of Science in the Department of Biology  
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By

Joshua James Traylor

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## ABSTRACT

Population surveys indicate a declining trend in abundance for the scoter genus at the continental level. Little is known about changes in life history traits responsible for the recent population decline of white-winged scoters (*Melanitta fusca deglandi*, hereafter scoters). Therefore, I studied nesting and duckling ecology of scoters at Redberry Lake, Saskatchewan, Canada during summers 2000-2001 when I found 198 nests. To examine nest-site selection, I compared habitat features between successful nests, failed nests, and random sites. Discriminant function analysis differentiated habitat features, measured at hatch, between successful nests, failed nests, and random sites; lateral ( $r = 0.65$ ) and overhead ( $r = 0.35$ ) concealment were microhabitat variables most correlated with canonical discriminant functions. I also modeled daily survival rate (DSR) of nests as a function of year, linear and quadratic trends with nest age, nest initiation date, and seven microhabitat variables. Nest survival from a time constant model (i.e., Mayfield nest success estimate) was 0.35 (95% CL: 0.27, 0.43). Estimates of nest success were lower than those measured at Redberry Lake in the 1970s and 1980s. In addition to nest survival increasing throughout the laying period and stabilizing during incubation, nest survival showed positive relationships with nest concealment and distance to water, and a negative relationship with distance to edge. Considering these factors, a model-averaged estimate of nest survival was 0.24 (95% CL: 0.09, 0.42). I conclude that scoters selected nesting habitat adaptively because (1) successful sites were more concealed than failed sites, (2) nest sites (i.e., successful and failed) had higher concealment than random sites, and (3) nest sites were on islands where success is greater than mainland.

I then estimated duckling and brood survival with Cormack-Jolly-Seber models, implemented in Program Mark, from observations of 94 and 664 individually marked adult hens and ducklings, respectively. I tested hypotheses about duckling survival and (1) hatch date, (2) initial brood size at hatch, (3) duckling size and body condition at hatch, (4) offspring sex, (5) maternal female size and body condition at hatch, and (6) weather conditions within one week of hatching. Most mortality occurred during the first six days of duckling age. Variation in both duckling and brood survival were best modeled with effects of hatch date and initial brood size, while effects of female

condition, female size, duckling size, and duckling condition were inconsistent. Survival probability clearly decreased with advancing hatch date and increased with larger initial brood sizes. Effects of weather and offspring sex in 2001, the only year such information was collected, suggested survival was negatively related to poor weather, but sex of ducklings, beyond size-related differences (i.e., sexual-size dimorphism), was unimportant. Estimates of survival to 28 days of age (30-day period), whether for ducklings (0.016, 0.021) or broods (0.084, 0.138) in 2000 or 2001, respectively, are the lowest of published studies and first for scoter broods in North America. I suspect intense gull predation shortly after hatch had the largest influence on duckling survival. Further research is needed to ascertain if low nesting success and duckling survival as well as other life cycle components are limiting scoter populations locally and throughout the rest of their breeding range.

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## **1. GENERAL INTRODUCTION**

### **1.1 POPULATION BIOLOGY AND LIFE HISTORY ATTRIBUTES**

Understanding how life history traits (i.e., natality, mortality, dispersal, and migration) affect population trends and identifying factors that regulate populations are major goals of population biology (Begon et al. 1996, Johnson 1996, Williams et al. 2002).

Populations are affected by biotic and abiotic factors such as weather, food availability, quality/quantity of habitat, predation, and disease (Lack 1954, Newton 1998, Williams et al. 2002). Consequently, fluctuations in populations can occur over time. Population fluctuations may result from changes in any or all components of life cycles (Caswell 2000). Thus, understanding ecological factors that influence specific vital rates can lead to an improved knowledge of processes responsible for population change.

In avian species, life cycles are composed generally of breeding probability, nesting success, offspring survival to fledge, juvenile survival, subadult survival, and adult survival. Population growth rate (i.e.,  $\lambda_t$ ) is equivalent to the sum of adult survival probability and recruitment rate (Nichols and Hines 2002). Populations can decrease ( $\lambda_t < 1$ ), increase ( $\lambda_t > 1$ ) or remain constant ( $\lambda_t = 1$ ) (Williams et al. 2002). In many waterfowl species, adult survival probability has the greatest potential influence on population growth (Flint and Grand 1997, Rockwell et al. 1997, Schmutz et al. 1997, Hoekman et al. 2002). Nevertheless, changes in recruitment can have important consequences for population change, especially if adult survival probability is high (Williams et al. 2002). Recruitment probability is defined as entry into the breeding population and is the product of breeding probability, clutch size, nesting success, and offspring survival to breeding age (i.e., offspring survival to fledge, juvenile survival, and subadult survival). Few studies have examined all components of recruitment (Hepp et al. 1989), despite the fact that this information is needed to fully understand causes of population change.

Estimation of all recruitment components can be difficult. Difficulty exists in estimating juvenile and subadult (e.g., nonbreeding) survival specifically if individuals remain on wintering areas until breeding age or if they can not be captured on breeding areas. Furthermore, in ducks it has been assumed that breeding probability is equivalent to one (i.e., birds breed each year) (Rohwer 1992), but recently Anderson et al. (2001) provided evidence that some birds forgo breeding in some years (see also Blums et al. 1996, Dufour and Clark 2002). Problems in estimation of these components persist because difficulty exists in following individuals from fledging to breeding and marking large numbers of birds for long periods of time. Components of recruitment such as clutch size, nesting success, and offspring survival to thirty days of age are easier to monitor and can be accurately obtained (Johnson et al. 1992), although nesting success and offspring survival to thirty days combined are often used as an index of recruitment in waterfowl (Cowardin and Johnson 1979, Cowardin and Blohm 1992, Grand and Flint 1997, Flint et al. 1998a).

Nesting success is a critical component of recruitment (Johnson et al. 1992) and can be affected by predation, weather, female body condition, female age, and nest-site placement (Afton and Paulus 1992, Johnson et al. 1992, Flint and Grand 1996). However, predation is the most important proximate cause of nest failure in birds (Martin 1995). Predation may have greater impacts on recruitment in species with limited or no renesting. Renesting probability in some species is low because they nest relatively late in the season and have a shortened breeding season, or endure substantial energetic constraints allocating nutrient reserves for egg laying (Korschgen 1977, Brown and Brown 1981, Flint and Grand 1996). Thus, nesting success may have a most important influence on recruitment of young into the breeding population (Johnson et al. 1992, Greenwood et al. 1995, Flint et al. 1998a). However, even with successful hatch, full broods can be lost thus rendering duckling survival a second limiting factor of recruitment (Johnson et al. 1992, Grand and Flint 1996).

Duckling survival can be a bottleneck for recruitment (Coulson 1984, see Flint et al. 1998b), being influenced by numerous factors such as adverse weather conditions, predation events, disturbance and separation events, and increased internal parasitic loads (Bourgeois and Threlfall 1982, Mendenhall and Milne 1985, Mikola et al. 1994,

but see Johnson 1992 for review). Duckling survival generally decreases with later hatch dates (Rotella and Ratti 1992b, Dzus and Clark 1998, Blums et al. 2002) and with smaller brood size (Kehoe 1989) though results are somewhat mixed (Dawson and Clark 1996, Guyn and Clark 1999). Furthermore, decreased female condition may reduce vigilance and brooding, and subsequent abandonment could make ducklings more susceptible to predators, poor nutrition in unfavorable habitats, and thermal stress (Makepeace and Patterson 1980, Mendenhall and Milne 1985, Rotella and Ratti 1992b). Survival is typically lowest during the first ten days after hatch in waterfowl with survival rates becoming constant by thirty days of duckling age (Orthmeyer and Ball 1990, Mauser et al. 1994, Grand and Flint 1996, Guyn and Clark 1999).

In the last twenty years, declining population trends of white-winged scoters (*Melanitta fusca deglandi*) in North America have caused concern. Collecting information on white-winged scoter life history traits to examine influences on population dynamics is necessary because they are among the least-studied of waterfowl (Brown and Fredrickson 1997). I studied nesting success and duckling survival in white-winged scoters, two important components of recruitment, with the goal of furthering our knowledge of breeding biology and population dynamics of this species and to begin developing a population model to aid in scoter conservation.

## **1.2 SCOTER POPULATION TRENDS**

Black scoters (*M. nigra*), surf scoters (*M. perspicillata*), and white-winged scoters are counted in aggregate during aerial surveys each spring in North America. Breeding ranges of the three species also show much overlap. Because of considerable sympatry, it is not possible to examine species-specific population trends over their entire range. Nevertheless, population surveys indicate a declining trend in abundance for this genus at the continental level (Kehoe et al. 1994, Trost 1998). North American scoter populations appear to have declined by ~ 65% since the 1950s with > 50% of the decline occurring over the last twenty years (Fig. 1.1) (Bellrose 1980, Trost 1998). Data from the breeding waterfowl survey for the southern survey strata represents primarily white-winged scoters based on scoter breeding ranges (e.g., white-winged scoter are the only species to breed in the prairie biome of western Canada). Data from

these strata suggest that white-winged scoters (hereafter scoter) have declined in Southern Saskatchewan and have become locally extinct in Southern Manitoba and Alberta (Fig. 1.2). Historically, the prairie biome was an important breeding area. Currently, the southern edge of their breeding range is north of the prairies, in the aspen parkland and declines are occurring there also. Breeding pair counts in the aspen parkland on Redberry Lake, Saskatchewan, have declined by about 45% in the last 20 years alone, while counts at Jessie Lake, Alberta, declined from 57 pairs to zero in the same amount of time (Brown and Brown 1981, P Kehoe, D.U. Canada and R. Alisauskas, CWS, pers. comm., D. Duncan, CWS, pers. comm.) suggesting northward retraction of the breeding range is continuing. Undoubtedly, scoters may soon disappear as breeding birds in the parkland ecoregion of western Canada with breeding areas relegated to the boreal forest, where population surveys also indicate declines (Fig. 1.2). There has been a 75% reduction in scoter population size since the 1950s in the boreal forest region of Alberta, British Columbia, and the Northwest Territories (Trost 1998).

Population decline could result from changes in any component(s) of the life cycle (e.g., adult survival, nesting success, or offspring survival) (Fig. 1.3). Therefore, all vital rates require estimation for a complete understanding of the relative contributions of separate life cycle components to population change. High annual adult survival rate (0.77), low production of  $\leq 1$  duckling/pair/year, depressed age ratios among harvested birds (series of age ratios  $< 0.6$  juveniles:adult, 1962-1992), and delayed sexual maturity of offspring suggest population declines may have resulted from low recruitment of ducklings into the breeding population (Brown and Brown 1981, Brown and Fredrickson 1989, Krementz et al. 1997). Thus, low productivity (i.e., duckling survival, and juvenile and subadult survival) could be important in the population dynamics of this species. Possible reasons for declines in scoter productivity include: high reliance on contaminated zebra mussels (*Dreissena polymorpha*) possibly leading to depressed likelihood of nesting by scoters (Di Guilo and Scanlon 1984), anthropogenic disturbance and habitat loss on breeding grounds (Brown and Brown 1981, Turner et al. 1987, and Mikola et al. 1994), increased gull (*Larus spp.*) populations (gulls are major predators of nests and ducklings) (Brown and Brown 1981,

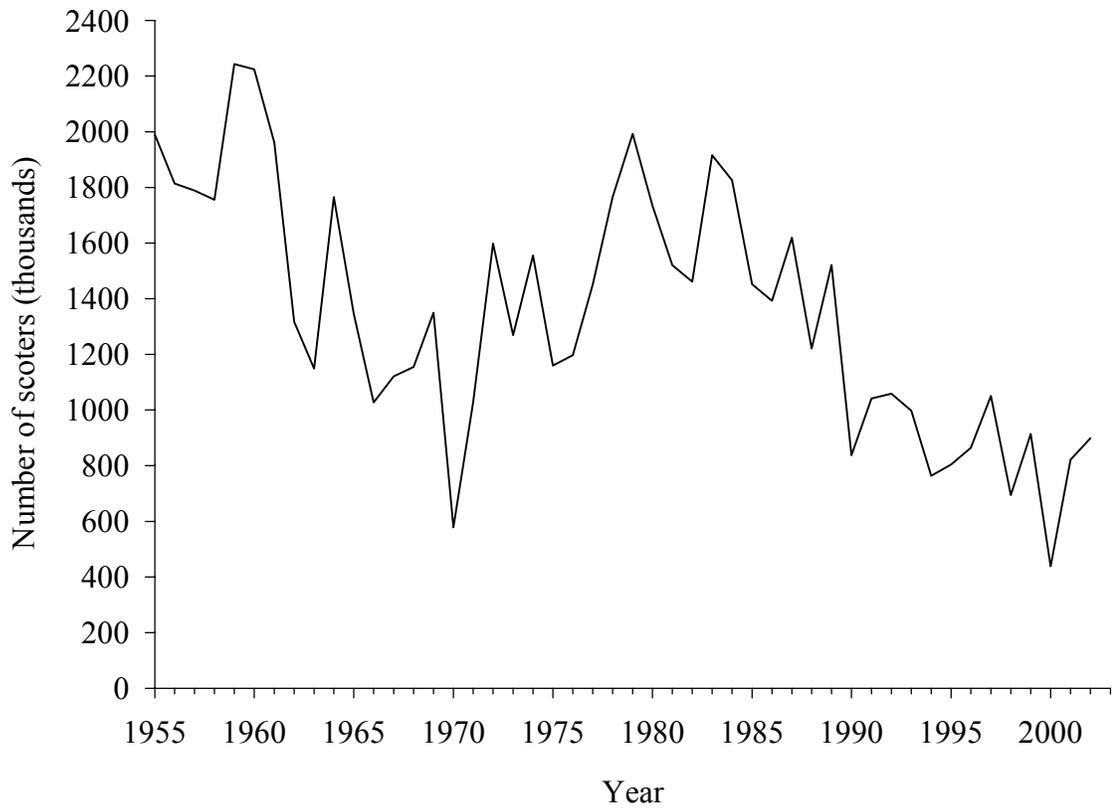


Figure 1.1. Combined populations of black (*Melanitta nigra*), surf (*M. perspicillata*), and white-winged (*M. fusca deglandi*) scoters during 1955-2002 for all strata in the breeding waterfowl survey in Western Canada (U.S. Fish and Wildlife Service unpubl. data).

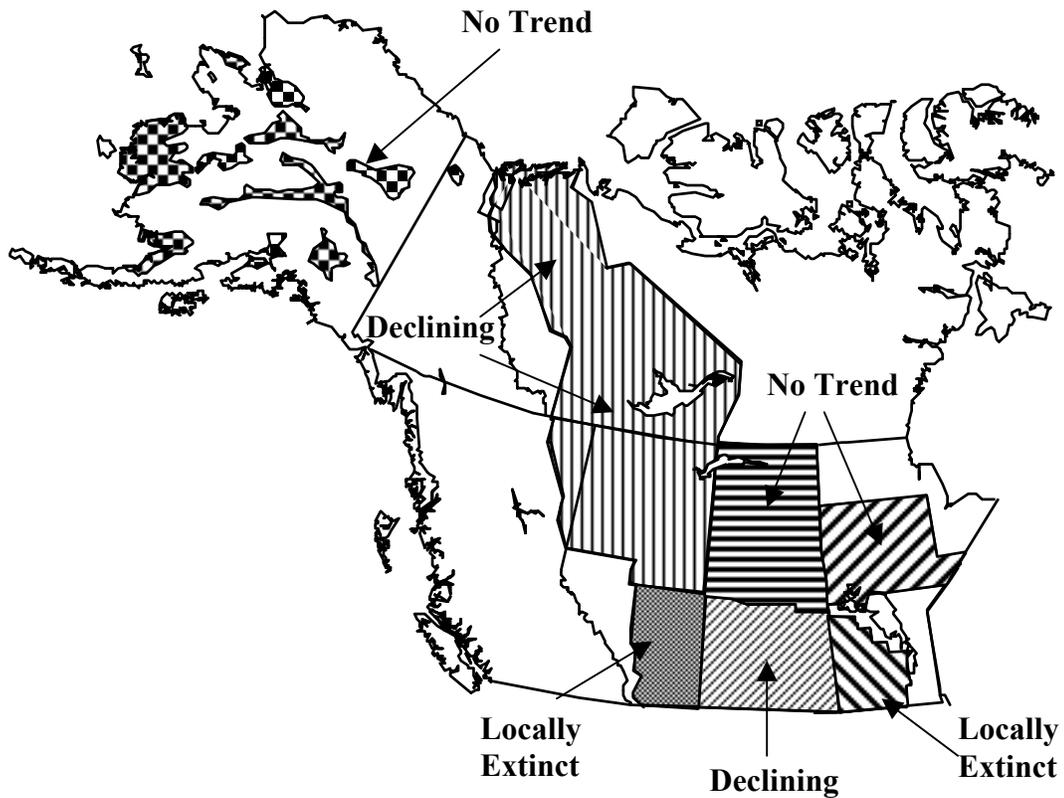


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Kehoe 1989) and increased harvest rates (Kehoe et al. 1994), all of which may result in decreased breeding probability, nesting success, and/or duckling survival. I focus on examining nesting success and offspring survival. Specific goals of my research are to identify factors that influence these components of the life cycle, and examine how current estimates compare to historic estimates. My research should complement other ongoing studies of survival probability in adult scoters, contribute a more complete picture of the life cycle, and provide a better understanding of scoter population dynamics.

### **1.3 THESIS FORMAT AND OBJECTIVES**

This thesis contains five main chapters, with chapters 3 and 4 focused on examining nesting success and duckling survival, respectively. The primary objective for chapter 3 was to estimate scoter nesting success in relation to nest initiation date and nest microhabitat variables. In addition, estimates of clutch size and nest success are compared with those from past studies (Brown 1981). The primary objective in chapter 4 was to estimate duckling and brood survival. Therein I present survival estimates of ducklings and broods in relation to factors such as hatch date, brood size, weather, female condition at hatch, female size, duckling sex, duckling size, and duckling condition.

Chapter 5 is a synthesis in which I discuss main conclusions from the thesis. I also discuss how my results for nesting success and duckling survival compared to historic data and how this might be relevant to scoter declines at Redberry Lake, Saskatchewan, and in other prairie/parkland breeding areas. I also recommend several key areas that future scoter research should address. Ultimately, this information, combined with future estimates of survival and productivity, can begin to provide better understanding of how components of the scoter life cycle influence population dynamics. Although this study does not address all aspects of the life cycle, it nevertheless represents an important advancement in scoter ecology. This information, with pending estimates from current studies, may contribute to future management and conservation decisions regarding scoters breeding at Redberry Lake and elsewhere.

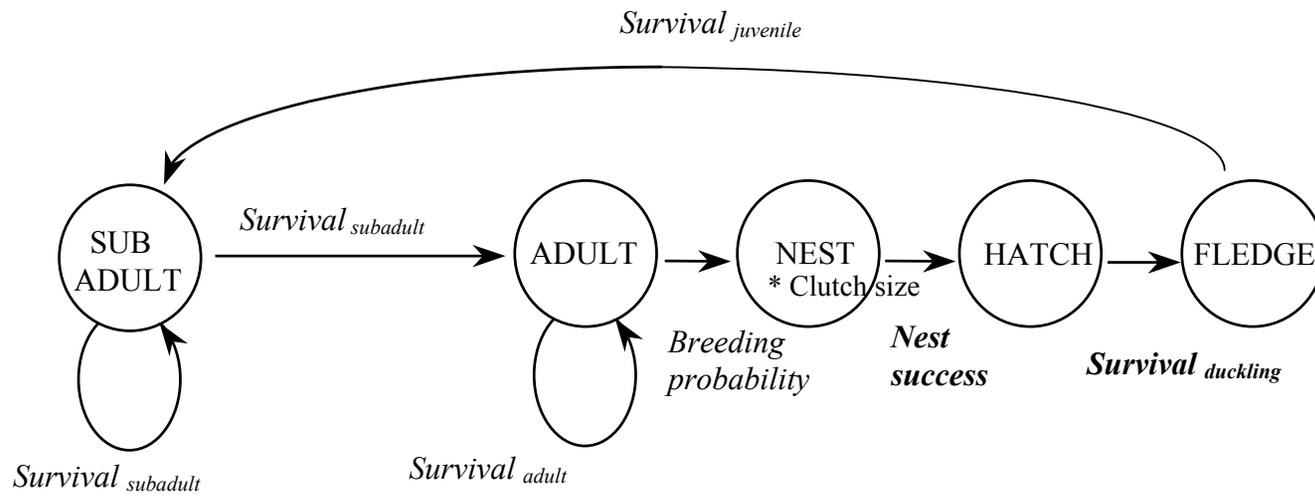


Figure 1.3. Conceptual life cycle diagram for white-winged scoters (*Melanitta fusca deglandi*).

Subadults can either remain subadults for 2 or 3 years, then become breeding adults. For this study I was interested in examining two important components of recruitment, nesting success and duckling survival.

## 2. STUDY AREA

Work was conducted on Redberry Lake, Saskatchewan (52°43' N, 107°09' W), about 100 km NW of Saskatoon, Saskatchewan, from May to October 2000 and 2001 (Fig. 2.1). Redberry Lake is a 4500 ha federal bird sanctuary and World Biosphere Reserve supporting the highest known local breeding population of scoters in North America (P. Kehoe, D.U. Canada, pers. comm.). Scoters have been studied at Redberry Lake from 1975-1980 (Brown 1977, Brown 1981) and 1984-1985 (Kehoe 1989). The lake is within aspen parkland habitat, characterized by rolling hills, numerous small wetlands, and small-grain agriculture (Brown 1981). Water levels have dropped 10 m since 1940 (Evans et al. 1995). Lake water is mesosaline (20-50 g/L) (total dissolved solids 20.9 g/L), characterized by depths of 1-3 m along shorelines, an average depth of 9.3 m, and maximum depth of 20 m as measured by sonar (pers. obs.).

There are three islands and one peninsula in the western portion of the lake, where most scoters nest: Gull Island (51 ha), Pelican Island (50 ha), New Tern Island (3 ha), and Old Tern peninsula (6 ha) (Fig. 2.1). Pelican and New Tern Island are currently connected by a land bridge. Dominant island and peninsula vegetation consists of grasses (*Poacea spp.*), northern gooseberry (*Ribes oxycanthoides*), rose (*Rosa spp.*), Canada thistle (*Cirsium arvense*), fire-weed (*Epilobium angustifolium*), field sowthistle (*Sonchus arvensis*), western snowberry (*Symphoricarpos occidentalis*), Saskatoon berry (*Amelanchier alnifolia*), willow (*Salix spp.*), thorny buffaloberry (*Shepherdia argentea*), silverberry (*Elaeagnus commutata*), and trembling aspen (*Populus tremuloides*). The lake is free of emergent vegetation. Fenelleaf pondweed (*Potamogeton pectinatus*) and common wigeon grass (*Ruppia maritima*) are the most abundant species of submerged vegetation growing in the sandy bottom (Brown 1981).

California gulls (*Larus californicus*), ring-billed gulls (*Larus delawarensis*), white pelicans (*Pelecanus erythrorhynchos*), double crested cormorants (*Phalacrocorax auritus*), and common terns (*Sterna hirundo*) inhabit New Tern Island (Brown 1981)

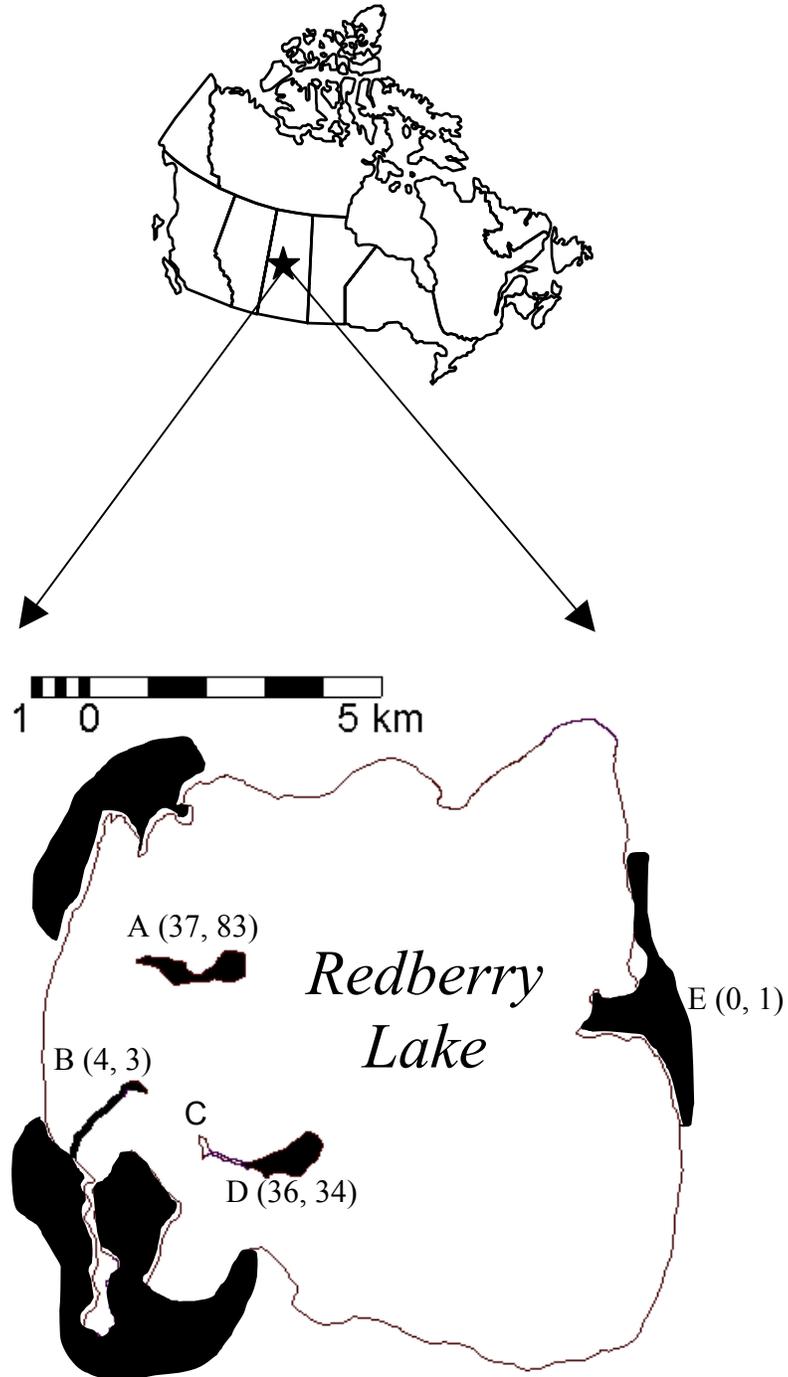


Figure 2.1. Redberry Lake federal bird sanctuary and Biosphere Reserve, Saskatchewan. Letters within the lake indicate (A) Gull Island, (B) Old Tern Peninsula, (C) New Tern Island, (D) Pelican Island, and (E) Mainland. Numbers in parentheses are number of nests located in 2000 and 2001, respectively. Shaded areas indicate islands and mainland areas searched for nests.

and, in addition, a colony of California and ring-gilled gulls persists on the north point of Pelican Island. Coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), great horned owls (*Bubo virginianus*), red-tailed hawks (*Buteo jamaicensis*), common crows (*Corvus brachyrhynchos*), and black-billed magpies (*Pica pica*) inhabit all the islands (pers. obs.). Further descriptions of the study area are given by Brown (1981) and by Kehoe (1989).

### **3. NESTING ECOLOGY OF WHITE-WINGED SCOTERS AT REDBERRY LAKE**

#### **3.1 INTRODUCTION**

Predation is the most important proximate cause of nest failure in birds (Martin 1995). Birds often adopt strategies to reduce predation risk by: (1) placing nests in sites not accessible to predators, (2) dispersing nests over vast areas to reduce likelihood of detection, (3) constructing cryptic nests in cover and maintaining behavioral crypsis, and (4) nesting in colonies, where ample food resources may satiate predators or where bird numbers may deter predators by aggression (Owen and Black 1990). However, most birds select a strategy that relies on decreased nest detection or accessibility by predators (Martin 1995).

One of the most important determinants of nest success is concealment or nest visibility (Martin 1995, Clark and Shutler 1999), which is related to specific vegetation characteristics such as density. Tall, dense vegetation may confer protection by creating visual barriers, increasing numbers of available nesting sites, and hindering mammalian predator movement (Livezey 1981, Martin 1993). Nest success also can increase with distance from habitat edge (Filliater et al. 1994) and water (Crabtree et al. 1989) because some predators actively search near such edges (Gates and Gysel 1978, Crabtree et al. 1989). Additionally, some studies suggest that nest success is higher for nests initiated earlier in the season because predation pressure is lower due to seasonally abundant alternative prey (Flint and Grand 1996). Hence, decisions about where and when to nest can be critical to nesting success.

Little is known about changes in life history traits responsible for the recent population decline of scoters (Sea Duck Joint Venture Management Board 2001). As part of an effort to begin to understand scoter population biology, my objective was to estimate two important components of recruitment (i.e., nesting success and duckling

survival) and understand the contribution of each to local population change. This chapter focuses on nesting success only. My first objective was to estimate nest initiation dates, clutch sizes, egg hatchability, and hatch dates of scoter nests. Secondly, to understand patterns of nest use and ongoing natural selection, I compared characteristics of successful nests, failed nests, and randomly-located sites (Clark and Shutler 1999). Thirdly, I estimated nest survival and compared current estimates to historic estimates from my study site. I also investigated the importance of microhabitat at nest sites and nest initiation date on daily nest survival rates. An examination of microhabitat features among successful and failed nests in areas with high depredation rates may facilitate understanding of the process of nest-site selection (Clark and Shutler 1999). I predicted that (1) earlier nesting, (2) higher concealment (lateral and/or overhead), (3) denser and taller vegetation, (4) farther distance from habitat edges, and (5) farther distance from water would be positive correlates of daily nest survival rates.

## **3.2 METHODS**

### **3.2.1 Nest searches**

Nest searches were conducted on three islands, and on portions of mainland near the eastern and western lake shores from early-June to mid-August, 2000-2001 (Fig. 2.1). No nest searching or other research activities occurred on New Tern Island where a white pelican (*Pelecanus erythrorhynchos*) colony was located. Nest searches were performed between 0700 and 2200 hrs. All island habitats and portions of the mainland were systematically searched on foot five times and three times per year, respectively. A nest was defined as a bowl with  $\geq 1$  egg. When a nest was found, its position was recorded using a global positioning system (GPS) to aid in relocation; eggs were then covered with nesting material to simulate natural incubation recesses by females (Götmark 1992). Clutch size (i.e., the number of eggs deposited) was recorded only for nests that survived to incubation. Nest initiation dates were estimated by subtracting stage of embryonic development (i.e., obtained by candling eggs) (Weller 1956) and clutch size (assuming 1 egg = 1.5 days; Brown and Brown 1981) from the day the nest was found. Incubation was assumed to be 28 days (Brown and Brown 1981). Nests were visited every 7-10 days to determine fate (i.e., successful, abandoned, depredated,

or unknown) but visitation intervals were changed so that nests were visited at the estimated hatch date (Flint and Grand 1996). Nests were considered successful if at least one egg hatched as indicated by the presence of egg membranes (Klett et al. 1996) or ducklings. Nests were considered depredated if there was evidence of mammalian (e.g., combination of presence of guard hair, nest bowl dug out, teeth marks in egg shell, and/or no yolk on shell) or avian (e.g., combination of presence of feathers, beak marks on shells, and/or yolk in/on shell) visitation. Nests were considered abandoned if no new eggs were deposited during laying or eggs remained cold and/or uncovered. Otherwise nest fate was classed as 'unknown'.

I assumed observer effects (i.e., human induced abandonment or predation) on nesting success were trivial because nests were visited infrequently and no nest markers were used in relocation. Additionally, measurement of nest-site vegetation was done after fate was ascertained (Krasowski and Nudds 1986, Clark and Shutler 1999) to reduce potential detrimental disturbance. Krasowski and Nudds (1986) suggested that investigator activity at nest sites might influence nest fate. Olson and Rohwer (1998) reasoned that repeated visits to nests might cause decreased success rates through indirect factors associated with human disturbance (see Rotella et al. 2000). Because of differences in frequency and timing of nest searches, historic nest success estimates from the 1970s/1980s may not be directly comparable to mine. I searched for nests beginning in early-June and found many nests during laying, especially during the 1 to 6 egg stage ( $n = 101$ ). Brown (1981) performed two searches of islands from 1977-1980, respectively, and began searches between 25 June and 20 July each year; my data suggested that because a disproportionate number of nests was depredated at the early laying stage, so Brown may have missed a substantial number of depredated nests and thus his estimates may have been biased high.

### **3.2.2 Nest microhabitat**

I measured seven microhabitat variables each year, within a 1 m<sup>2</sup> quadrat centered on the nest and random sites. Maximum live and dead vegetation heights were measured separately and directly over the nest (nearest cm with a meter stick). I measured both live and dead height because I predicted that dead height could provide primary cover

when nests were initiated, but then live vegetation height would provide additional cover as new vegetation grew. Vegetation density was taken as the number of stems/m<sup>2</sup> within the quadrat. Overhead concealment (%) was an index taken 1 m directly above nests by inserting a black cardboard disc with five 6.5 cm<sup>2</sup> squares into the nest bowl and estimating the average percentage of each white square that was obstructed from eye level directly above (Clark and Shutler 1999). Lateral concealment (%) was an index taken at ground level 1 m from nests by determining percentage of each nest obstructed in each cardinal direction; a concealment score was then computed as a mean value from each direction (Brua 1999). Distance to nearest edge (m) was estimated using a meter stick to the nearest point where a visible change in plant community was judged to occur (e.g., opening, shrub patch); hence this was a fine-grained measure relative to that used by Clark and Shutler (1999). Distance to nearest water (m) was measured directly by counting approximately 1 m paces (JJT).

### **3.2.3 Random sites**

Distance and cardinal directions of random locations from nests were selected using a random number table. Random numbers were assigned to eight directions (N, NE, E, SE, S, SW, W, NW) and a random number between 0 and 200 m was the distance from the nest. This approach for selecting random plots was reasonable because scoters nested throughout all island habitats and the maximum distance of a nest from water was about 200 m. When the location was reached, a rock was thrown over the shoulder to determine the random site. New points were selected when a random site occurred in water or on sand because scoter nests were never found at such sites (pers. obs.).

### **3.2.4 Statistical analyses: Nest-site selection**

General linear models (PROC GLM, SAS Institute 1989) were used to test for annual differences in nest initiation dates, egg hatchability, and hatch dates. I used a G-test to test for annual differences in clutch sizes. Linear regression was used to estimate changes in clutch size and egg hatchability with advancing nest initiation date. All linear trends were confirmed by visual inspection of data plots.

Nests that were found abandoned ( $n = 9$ ) and ‘dump’ nests ( $n = 2$  containing 17 and 19 eggs) were excluded because date of fate and nest initiation date could not be determined. Habitat variables were assessed for normality by examining skewness and kurtosis, plotting data, and assessing Shapiro Wilks’ test statistics (PROC UNIVARIATE, SAS Institute 1989). Maximum live and dead vegetation height, lateral concealment, and distance to water were square-root-transformed. Vegetation density and distance to edge were log-transformed. No improvement in normality was observed in overhead concealment after transformation (Shapiro Wilks’ test statistic = 0.90) so analyses proceeded on untransformed data. Nest initiation date was normally distributed.

Principal component analysis (PCA; PROC PRINCOMP, SAS Institute 1989) was used to test for multicollinearity among the seven nest-site variables. The first principal component explained about the same variation (35%) as would occur by chance alone (37%) (Legendre and Legendre 1983, Jackson 1993). Thus, I used all seven nest-site variables in a discriminant function analysis (DFA). DFA was used to determine characteristics that best discriminated between successful nests, failed nests (i.e., destroyed or abandoned) and random sites (Krasowski and Nudds 1986, Clark and Shutler 1999).

When performing DFA, I was interested only in examining habitat differences between groups. Therefore, I tested for yearly and seasonal differences in habitat characteristics before combining data for both years. To control for seasonal influences on the seven nest-site variables I saved residuals from an analysis of covariance with habitat measurements as dependent variables and date (i.e., days since January 1 that vegetation was measured) as the explanatory variable. Because there were yearly differences in nest-site variables, I created z scores (standard normal deviates) within years for residuals of each vegetation variable, thus controlling for year effects (Clark and Shutler 1999). Two DFAs were conducted both with and without abandoned nests classified as failed nests. Because quantitative results were similar, results from the analysis of larger sample size (i.e., combining abandoned and depredated nests as failed nests) are reported here.

### 3.2.5 Statistical analyses: Nesting success

Because nest microhabitat data were uncorrelated, I used all nest-site variables and nest initiation date as additive covariates in models of nest survival with Program MARK (White and Burnham 1999, but see Dinsmore et al. 2002). Program MARK nest survival allows for estimation of overall nest success as the product of daily nest survival across the 49-day laying and incubation period for scoters (Dinsmore et al. 2002). Habitat data used in DFA (i.e., corrected for seasonal effects and annual differences in habitat variables) were also used for analysis of nest survival.

I used an information theoretic approach for model selection (Burnham and Anderson 1998). I used the logit-link function to force all estimates of daily survival rate (DSR) to the parameter space between 0, 1 (Lebreton et al. 1992). Akaike's Information Criterion (AICc, adjusted for sample size, Akaike 1973) was used to select the best approximating model(s). A total of 11 candidate models, based on questions of interest (Burnham and Anderson 1998), were considered in a two-step process of model selection. First, I considered models without covariates where daily survival rate (DSR) showed temporal trends over the nesting cycle (i.e., with nest age). My assessment of temporal variation in nest age was done by comparing fit of models with DSR that was either (1) constant over the 49-day nesting cycle,  $\{S.\}$ , (2) constant over the 49-day nesting cycle in each year (i.e., testing annual differences,  $\{S_{\text{year}}\}$ ), (3) showed a linear trend over the nesting cycle,  $\{S_A\}$ , or (4) included a quadratic trend over the nesting cycle to accommodate some complexity  $\{S_{A+A^2}\}$  (Dinsmore et al. 2002). I did not want to over-fit the data, so I did not fit more complex age trend models.

The second step involved fitting covariates, to consider additional structure to DSR, to the most parsimonious model so far  $\{S_{A+A^2}\}$ . First, I considered fit of DSR to linear  $\{S_{A+A^2+\text{nid}}\}$  and quadratic  $\{S_{A+A^2+\text{nid}+\text{nid}^2}\}$  trends in nest initiation date. Then I considered all seven nest habitat variables as covariates to the most parsimonious model at that stage [i.e., live vegetation height (l), dead vegetation height (d), overhead concealment (oc), lateral concealment (lc), vegetation density (vd), distance to edge (e), and distance to water (w)],  $\{S_{A+A^2+\text{nid}+l+d+\text{oc}+\text{lc}+\text{vd}+e+w}\}$ . If the 95% CI of  $\hat{\beta}_1$ , a covariate, on the logit scale included zero, the precision of the estimate was considered to be low and it was removed from the model. Finally, I examined if model fit would improve by

reconsidering covariates that only just included zero (e.g., -0.07 to 1.33) in the 95% CI of  $\hat{\beta}_1$ , singularly and combined. Only additive models without interactions were considered. I used model weight ( $w_i$ ) to evaluate likelihood of each model; to accommodate model uncertainty, I used model-averaged estimates from the candidate model set to draw inferences about variation in DSR (Burnham and Anderson 1998).

All covariates were standardized by Program MARK; each covariate had a mean of zero and ranged from -3 to 3. Confidence limits of nest success were estimated using the nest survival function in Program MARK (White and Burnham 1999, Dinsmore et al. 2002). Unless otherwise indicated, tests were two-tailed with significance levels set at  $P < 0.05$ . All analyses were executed using SPSS (1999), SAS (1989), or Program MARK (White and Burnham 1999). This project was approved under permits issued by the University of Saskatchewan's Committee on Animal Care on behalf of the Canadian Council on Animal Care and Canadian Wildlife Service.

### **3.3 RESULTS**

#### **3.3.1 Nesting ecology**

I found 77 nests in 2000 and 121 nests in 2001 (Table 3.1) and all but one were on islands (Fig. 2.1). Females were seen flying to locations in mainland habitat but I found only one active and two apparently failed nests from previous years during 40 h of searching mainland habitats. Nest densities for areas searched on islands averaged 0.70 and 1.1 nests/ha in 2000 and 2001, respectively, while nest densities for area searched on the mainland (~ 900 ha) were 0 and ~ 0 nests/ha in 2000 and 2001, respectively. Nest initiation dates for all nests ranged from 7 June to 6 July, 2000, and 10 June to 11 July, 2001 (Table 3.1). There were no differences in nest initiation ( $F = 1.88$ ,  $df = 1$ , 185,  $P = 0.17$ ) or hatch ( $\bar{x} = 30$  July, 95% CI: 29 - 31 July) ( $F = 0.14$ ,  $df = 1$ , 107,  $P = 0.75$ , Table 3.1) dates between years. Mean clutch size was 8.8 (95% CI: 8.6 - 9.1, Table 3.1) and declined by 0.11 (95% CI: 0.08 - 0.14) eggs/day during the nesting season ( $F = 40.44$ ,  $df = 1$ , 138,  $r^2 = 0.23$ ,  $P \leq 0.0001$ ). When grouped into small (5-8 eggs), medium (9 eggs) and large (10-13 eggs) clutches, clutch size varied between years; in 2000 there were more nests with larger clutch sizes (48%) than in 2001

Table 3.1. Number of nests, mean initiation dates, mean clutch size, mean hatch date, mean egg hatchability (% of eggs that hatch per nest), and nesting interval length for white-winged scoters at Redberry Lake, Saskatchewan, Canada, 1977-1980 and 2000-2001. Historic data are taken from Brown (1981).

Parameter	1977	1978	1979	1980	2000	2001
Number of nests	89	101	132	104	77	121
Nest initiation date <sup>a</sup>	-	-	-	-	19 June (171) <sup>b</sup>	22 June (173)
95% CI	-	-	-	-	17 - 22 June	21 - 23 June
<i>n</i>	-	-	-	-	73	114
Nest initiation date <sup>c</sup>	13 June (164)	15 June (166)	17 June (168)	15 June (166)	18 June (170)	20 June (171)
95% CI	11 - 15 June	13 - 16 June	16 - 18 June	14 - 16 June	15 - 19 June	18 - 22 June
<i>n</i>	73	70	102	71	44	65
Clutch size	9.1	8.7	9.3	8.3	9.1	8.7
95% CI	8.6 - 9.6	8.2 - 9.2	8.9 - 9.7	7.9 - 8.7	8.7 - 9.5	8.4 - 8.9
<i>n</i>	73	70	102	71	44	65
Hatch date	21 July (202)	23 July (204)	26 July (207)	21 July (202)	29 July (211)	31 July (212)
95% CI	19 - 23 July	22 - 24 July	25 - 27 July	20 - 21 July	28 - 30 July	30 - 1 August
<i>n</i>	73	70	102	71	44	65

Table 3.1 continued

Egg hatchability (%)	81.3	83.9	72.0	89.1	84.5	84.5
95% CI	73.6 - 86.8	77.0 - 88.5	66.7 - 77.4	83.1 - 95.2	78.7 - 90.2	79.5 - 89.5
<i>n</i>	73	70	102	71	44	65
Interval <sup>d</sup>	38	38	39	36	41	41

<sup>a</sup> Mean nest initiation date for successful and failed nests.

<sup>b</sup> Number in parentheses is julian date (164 = 13 June)

<sup>c</sup> Mean nest initiation date for successful nests.

<sup>d</sup> Interval in days between mean initiation date and mean hatch date for successful nests.

(25%), while in 2001 there were more small clutches (43%) than in 2000 (29%) ( $G = 6.21$ ,  $df = 2$ ,  $P = 0.04$ ). Mean egg hatchability was 84.5% (95% CI: 80.8 - 88.2%), with no annual change ( $F = 0.00$ ,  $df = 1$ , 107,  $P = 0.99$ ) (Table 3.1). Egg hatchability declined by 1.1%/day (95% CI: 0.5 - 1.7) during the nesting season ( $F = 11.46$ ,  $df = 1$ , 107,  $r^2 = 0.10$ ,  $P \leq 0.0001$ ).

### 3.3.2 Nest-site selection

Scoters nested predominantly in northern gooseberry. Rose, grasses, Saskatoon bushes, wild mustard (*Brassica kaber*), and western snowberry or a combination of these species were present less frequently than northern gooseberry within quadrats centered on the nest. DFA revealed clear differences in habitat among sites (Wilks' Lambda,  $U = 0.54$ ,  $P < 0.0001$ ), and correctly classified 78.9% of successful nests, 12.8% of failed nests, and 86.6% of random sites. A higher proportion of failed nests were misclassified as successful nests than random sites (Fig. 3.1), although the overall correct classification rate was 69.0%, which was better than chance alone (Kappa = 0.48, 95% CI: 0.40 - 0.58, chance corrected,  $z = 11.1$ ,  $P < 0.0001$ ) (Titus et al. 1984).

The first discriminant function explained 97.9% of the variation in the data, so the second discriminant function was not considered. Lateral ( $r = 0.65$ ) and overhead ( $r = 0.35$ ) concealment were original variables most strongly correlated with canonical discriminant functions, producing the largest differences among groups (Table 3.2). Nests (i.e., both successful and failed nests) had more lateral and overhead concealment than random sites which strongly suggested nonrandom habitat selection (Fig. 3.1). Furthermore, failed nests had ~ 3 times less lateral, and ~ 2 times less overhead concealment than successful nest sites suggesting strong selection against nests with low concealment (Fig. 3.1 and Table 3.2).

### 3.3.3 Nesting success

I suspect that ~ 9.6% and ~ 22.8% of nests that I detected were depredated by avian predators in 2000 and 2001, respectively. Additionally, I estimated that roughly 17.8%

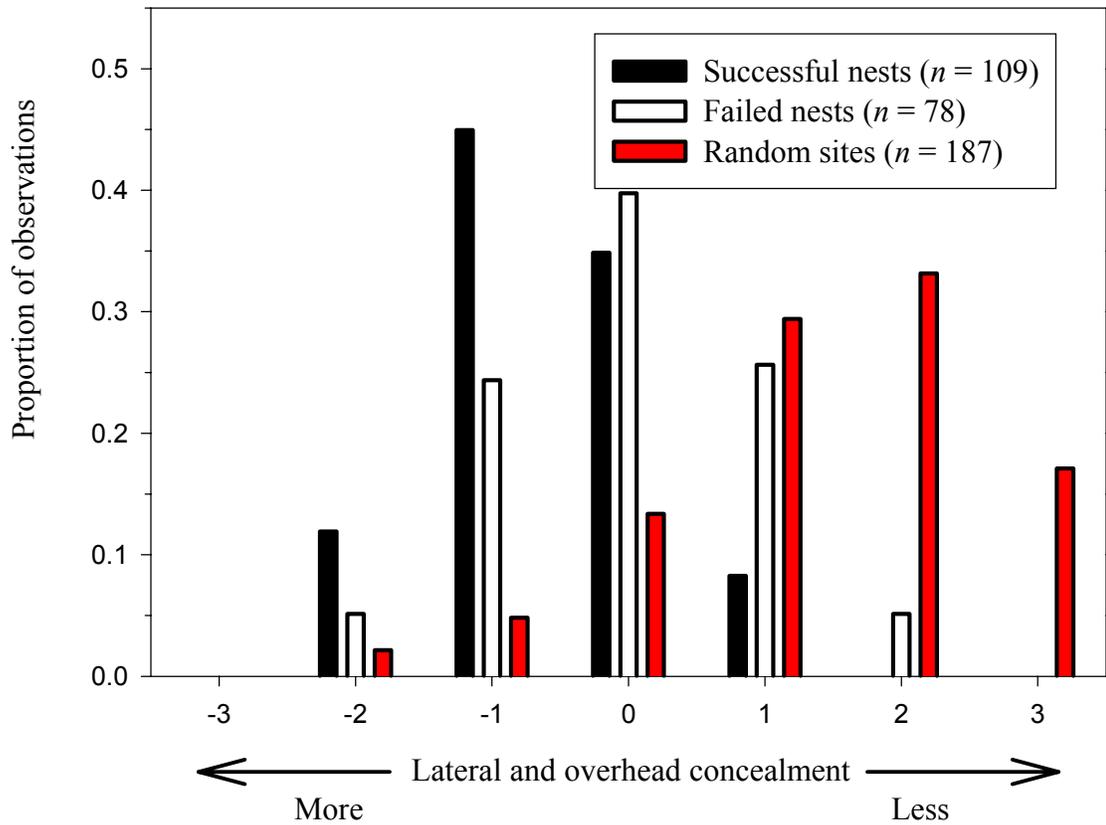


Figure 3.1. Distribution of discriminant function scores for successful and failed nests of white-winged scoters and random sites at Redberry Lake, Saskatchewan, 2000-2001. Lateral ( $r = 0.65$ ) and overhead ( $r = 0.35$ ) concealment were listed below the abscissa in order of decreasing importance and were listed because loadings  $\geq |0.35|$ .

Table 3.2. Nest-site variables for successful and failed white-winged scoter nests and random sites and the corresponding correlation coefficient with the first canonical discriminant function.

Nest-site Variables	Successful Nests ( <i>n</i> = 109) <sup>a</sup>	Failed Nests ( <i>n</i> = 78)	Random Sites ( <i>n</i> = 187)	DFA Correlation Coefficients <sup>f</sup>
Live height (cm)	90.33 ± 7.42 <sup>b</sup>	85.73 ± 14.68	59.17 ± 5.14	-0.15
Dead height (cm)	46.74 ± 5.95	50.98 ± 7.92	34.92 ± 4.97	-0.28
Overhead Concealment (%) <sup>c</sup>	<b>20.64 ± 4.36<sup>d</sup></b>	<b>41.62 ± 6.92</b>	<b>69.12 ± 4.56</b>	0.35
Lateral Concealment (%) <sup>e</sup>	<b>11.69 ± 2.65</b>	<b>31.20 ± 5.81</b>	<b>62.92 ± 4.72</b>	0.65
Distance to Edge (m)	1.03 ± 0.12	1.07 ± 0.15	1.57 ± 0.18	0.14
Distance to Water (m)	113.44 ± 8.97	101.53 ± 11.15	105.2 ± 7.84	-0.02
Vegetation density (stems/m <sup>2</sup> )	37.97 ± 3.67	37.68 ± 6.12	58.41 ± 9.59	0.04

<sup>a</sup> Sample size

<sup>b</sup> Mean ± 95% confidence interval

<sup>c</sup> Lower values for overhead concealment signify greater concealment.

<sup>d</sup> Bold values represent significant differences (no overlap of 95% CI) among the three groups.

<sup>e</sup> Lower values for lateral concealment signify greater concealment.

<sup>f</sup> Coefficients less than |0.35| were deemed unimportant.

and 8.8% of nests were depredated by mammalian predators and 12.3% and 10.5% were abandoned in 2000 and 2001, respectively; overall apparent nest success was 60.3% (44/73) and 57.0% (65/114) in 2000 and 2001, respectively. Only 1 nest was classed as unknown fate in 2001.

From my comparison of candidate models, Mayfield nest success was 0.35 (95% CL: 0.27, 0.43) from model {S .} containing only an intercept term for DSR (Table 3.3). Mayfield nest success calculated for each year from model {S<sub>year</sub>} was 0.37 (95% CL: 0.25, 0.50) in 2000 and 0.34 (95% CL: 0.24, 0.43) in 2001, suggesting no difference in nest survival between years. However, both of these simple models had poor performance when compared to more complex models in the candidate set. My model-averaged estimate of nest survival was slightly lower at 0.24 (95% CL: 0.09, 0.42), suggesting that simple Mayfield estimate could be biased by about ~ 0.10. Models with quadratic trends with nest age had stronger support than models with either linear or constant effects over the nesting cycle (Table 3.3). Daily nest survival increased throughout the laying period and was lower during the first 6 days relative to days 11-13 of the nesting cycle (Fig. 3.2). Daily nest survival was higher throughout the first 28 days of incubation than during the first week of laying (Fig. 3.2). A model with DSR as a linear function of nest initiation date had stronger support than a model with DSR as a quadratic function of nest initiation date (Table 3.3). DSR decreased with increasing nest initiation date (i.e., from {S<sub>A+A<sup>2</sup>+nid</sub>}). I estimated  $\hat{\beta}_{ND} = -0.21$ , 95% CL: -0.45, 0.03, although the 95% confidence interval just included zero.

When all covariates were added to model {S<sub>A+A<sup>2</sup></sub>}, model quality improved by 14.5 AIC<sub>c</sub> units (Table 3.3). DSR from the most parsimonious model suggested that nest survival was a function of overhead concealment, lateral concealment, distance to edge, and distance to water (Table 3.3). Nest survival increased with increasing overhead and lateral concealment ( $\hat{\beta}_{OC} = -0.38$ , 95% CL: -0.66, -0.11 and  $\hat{\beta}_{LC} = -0.26$ , 95% CL: -0.57, 0.04), closer to habitat edges ( $\hat{\beta}_E = -0.24$ , 95% CL: -0.48, 0.00), and farther from water ( $\hat{\beta}_W = 0.29$ , 95% CL: 0.05, 0.53), though confidence

Table 3.3. Summary of model selection results for factors influencing white-winged scoter nest survival at Redberry Lake, Saskatchewan, Canada, 2000-2001 ranked by ascending  $\Delta AIC_c$ .

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	$\Delta AIC_c$ <sup>c</sup>	$w_i$ <sup>d</sup>	K <sup>e</sup>	Deviance <sup>f</sup>
{S <sub>A+A<sup>2</sup>+oc+lc+e+w</sub> }	441.01	0.00	0.41	7	426.67
{S <sub>A+A<sup>2</sup>+oc+e+w</sub> }	441.88	0.87	0.26	6	429.62
{S <sub>A+A<sup>2</sup>+oc+lc+w</sub> }	442.51	1.49	0.19	6	430.25
{S <sub>A+A<sup>2</sup>+oc+w</sub> }	443.49	2.48	0.12	5	433.31
{S <sub>A+A<sup>2</sup>+nid+l+d+oc+lc+vd+e+w</sub> }	447.48	6.47	0.02	11	424.66
{S <sub>A+A<sup>2</sup>+nid</sub> }	461.16	20.15	0.00	4	453.04
{S <sub>A+A<sup>2</sup></sub> }	462.01	20.99	0.00	3	455.93
{S <sub>A+A<sup>2</sup>+nid+ nid<sup>2</sup></sub> }	462.96	21.95	0.00	5	452.78
{S <sub>A</sub> }	469.15	28.14	0.00	2	465.12
{S}	537.57	96.56	0.00	1	535.56
{S <sub>year</sub> }	539.35	98.33	0.00	2	535.31

<sup>a</sup> Model factors included linear trend with age (A), quadratic trend with age (A+A<sup>2</sup>), constant daily survival (.), nest initiation date (nid), quadratic nest initiation date (nid + nid<sup>2</sup>), live vegetation height (l), dead vegetation height (d), overhead concealment (oc), lateral concealment (lc), vegetation density (vd), distance to edge (e), and distance to water (w).

<sup>b</sup> Akaike's Information Criterion with small sample correction.

<sup>c</sup> Difference in AIC<sub>c</sub> values between the model with the lowest AIC<sub>c</sub> value.

<sup>d</sup> Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

<sup>e</sup> Number of estimable parameters.

<sup>f</sup> Deviance is difference between  $-2\log$ -likelihood of the current model and that of the saturated model.

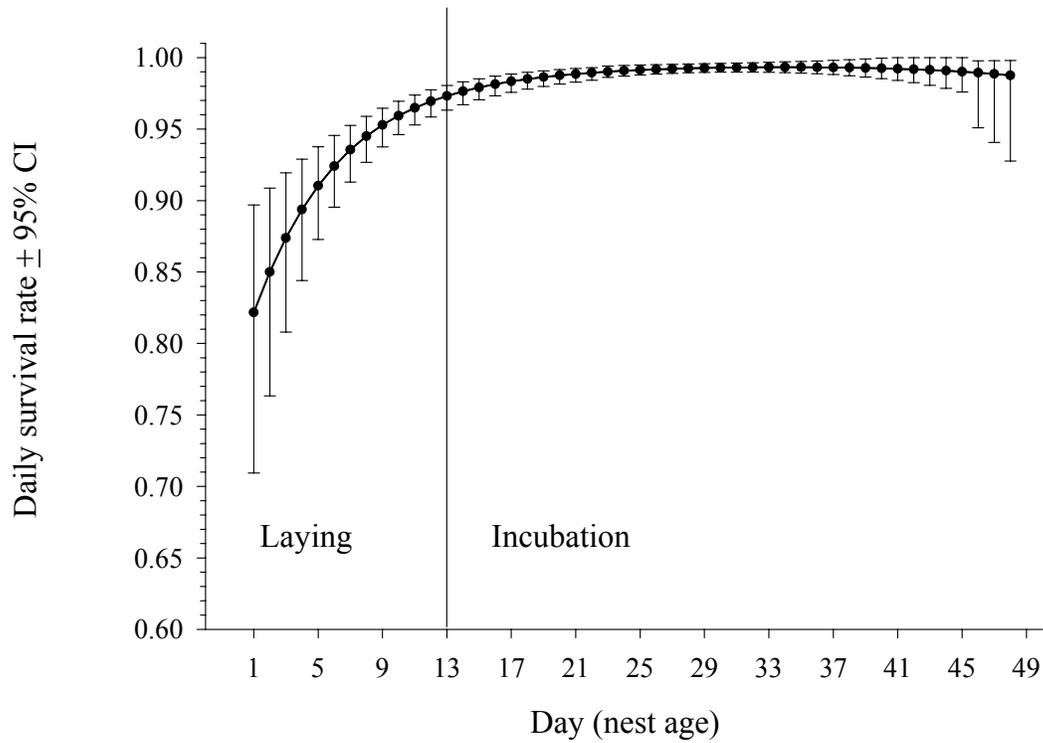


Figure 3.2. Daily survival rate of white-winged scoter nests during laying and incubation at Redberry Lake, Saskatchewan for 2000 ( $n = 73$ ) and 2001 ( $n = 114$ ), combined. Estimates  $\pm$  95% CI were obtained using weighted averages based on a candidate model set and were weighted according to  $AIC_c$  values from each model.

limits for  $\hat{\beta}_{LV}$  and  $\hat{\beta}_E$  just included zero. Models with  $\Delta AIC_c < 2$  had a cumulative weight of 86% (Table 3.3). There was no support for the importance of nest initiation date, maximum live and dead vegetation height, and vegetation density on nest survival, although inclusion of these effects improved model fit (Table 3.3).

### 3.4 DISCUSSION

#### 3.4.1 Nesting ecology

Compared to historic values (Brown 1977, Brown 1981), initiation dates and hatch dates for successful nests were later in my study (Table 3.1) and in 2002 (initiation date  $\bar{x} = 18$  June, 169 Julian and hatch date  $\bar{x} = 29$  July, 95% CI: 27 - 30 July, Julian date 210, and interval length was 41 days, C. Swoboda, Dept. of Biol., Univ. of Saskatchewan, pers. comm.). Later hatch dates were a result of not only later nest initiation, but also protracted nesting interval (Table 3.1). I hypothesize that such delayed and prolonged nesting are related to changes in nutrition (e.g., food related stress). Nesting female scoters rely on nutrient reserves stored before nesting for completion of incubation, but rely on exogenous nutrient for egg formation (Dobush 1986). Clutch size was unchanged from historical levels, but the source of these nutrients may have changed from completely exogenous to endogenous supplements, at the expense of nutrient reserves previously used for incubation, as found by Dobush (1986). Thus, if scoters now return to Redberry Lake in poorer condition than formerly, then more time might be required before nesting to store nutrient reserves for incubation. As well, food availability at Redberry Lake may have declined due to changing lake dynamics further impinging on ability of scoters to complete incubation. Lake water levels have dropped 10 m since 1940 and salinity levels (i.e., total dissolved solids 20.9 g/L) are approaching tolerance limits of amphipods (Hammer et al. 1990, Evans et al. 1995). *Gammarus*, once very abundant in the Redberry Lake ecosystem, are now thought to be rare if not extinct (Hammer et al. 1990). Furthermore, *Hyallela azteca*, the primary food of scoters at Redberry Lake and nearby lakes, also may have decreased because of elevated salinity levels (Hammer et al. 1990) or low water levels. Lower water levels mean some lakes (i.e.,  $\leq 2$  m deep) now freeze to the bottom killing amphipods (Lindeman and Clark 1999). Additionally, increasing salinity levels may

compromise the ability of females to assimilate nutrients and feed properly. In turn, reduction in nutrient reserves may motivate more frequent incubation recesses to supplement energy requirements needed to successfully complete incubation. The prolonged incubation period may also be related to the introduction of predators on historically predator free islands, although this is an unlikely response because females should decrease the length of incubation to curtail nest exposure to predators. Thus, compared to previously, protracted nesting intervals could have resulted from a combination of diminished daily rate of egg laying or prolonged incubation.

Delayed nesting and prolonged interval between nest initiation and hatch could impinge on female fitness in at least three ways. First, nest success of females in poor condition may be compromised because of decreased nest attentiveness, resulting in slower embryo development and higher predation rates because of longer nest exposure (Afton and Paulus 1992, Tombre and Erikstad 1996). Second, breeding season survival could decline because nesting females are exposed to predation pressure for longer periods. Finally, later hatch could reduce duckling survival (Guyn and Clark 1999, Chapter 4). Later hatch dates and longer development period (8 - 10 weeks) may expose scoter ducklings to adverse weather conditions as well as lower food resources during late summer and fall (Brown 1981, unpubl. data). Nevertheless, unpredictable adverse weather events, coupled with intense gull predation, seasonal decrease in food resources, and decreased hen vigilance all may reduce duckling survival and increase in importance during years of later hatch (Mendenhall and Milne 1985, Erikstad et al. 1993).

### **3.4.2 Nest-site selection**

My results suggest that nest concealment was the most important determinant of nest placement by scoters at Redberry Lake, and survival was positively related to concealment. My results were consistent with Brown (1977, 1980) in that females selected vegetation providing high concealment, primarily northern gooseberry and rose, and island habitats for nest sites. Successful sites typically had higher concealment, which presumably decreased probability of detection by predators and may have improved survival of nesting females (Sargeant and Raveling 1992). Brown

(1981) stated that experienced females with better concealed nests had higher nest success, while inexperienced females tended to select sites with less concealment and had lower nest success. Importantly, disproportionate amounts of concealment (i.e., combination of high vegetation density and cover) may be a selective disadvantage because escape response and view of nest surroundings are impaired; perhaps females select sites not with high vegetation density but with high cover (Table 3.2). Overall, well-concealed nest sites could be important to scoters because of their long egg-laying period, decrease in nest attentiveness as incubation progresses, and vulnerability to predators because of their slow escape behavior when flushed from nests (Brown 1981, unpubl. data).

My study shed light on both the pattern and process of nest-site selection in birds at two scales. Besides the propensity to nest in vegetation that provides high concealment, another adaptive strategy for nest placement by scoters included a propensity to nest on islands: compared to 197 nests found on islands, only one was found on searched mainland habitats that were far greater in area than searched areas on islands (Fig. 2.1). I feel that this comparison was valid because habitat was similar between islands and mainlands and detection probability of active nests by observers should have been the same. Nest survival is generally higher for ducks on islands than on mainland areas (e.g., Lokemoen and Woodward 1992, Clark and Shutler 1999).

My results are consistent with those of some studies that suggested that nest concealment was the most important factor discriminating between successful and failed nests (Crabtree et al. 1989, Martin 1992), though it is not always the case (Clark and Shutler 1999). I believe that nest predation was the selective force involved in the preference for well-concealed sites in this species because concealment differentiated between selected sites and random sites and between successful nests and failed nests (Martin 1993, Clark and Shutler 1999). Accordingly, as for birds in general, persistence of adaptive nest placement by scoters likely is associated with (1) high site fidelity by successful females, (2) natal philopatry, (3) social attraction between nesting females, (4) dispersal of failed nesters from sinks to sources, or (5) learned recognition by females of safe habitats (Pulliam 1988, Clark and Shutler 1999).

Nesting cover that provides high concealment may be more important to nest survival if predators are birds because they rely primarily on visual cues for detection of prey (Clark and Nudds 1991, Stokes and Boersma 1998). Concealment should be less important against mammalian predators that rely more on olfaction than do birds (Colwell 1992, Schieck and Hannon 1993). However, vegetation that provides high concealment may still reduce likelihood of nest detection by affording visual and olfactory protection (Martin 1993). High concealment may also impede movement of terrestrial predators and hinder search efficiency, further impinging on ability to detect prey (Martin 1992, 1993). My results suggest that lateral and overhead concealment reduced predation risk from both mammals and birds because successful nests were more concealed than failed nests. Thus, selection of a well-concealed nest sites can still be an effective deterrent even if there is a rich guild of predators (Filliater et al. 1994). Perhaps predation attempts by mammals were only incidental (Vickery et al. 1992), an artifact of differences in foraging techniques and search efficiencies of the predator community (Clark and Nudds 1991) or type of available buffer prey (Klett and Johnson 1982). Factors such as thermal regimes (Gloutney and Clark 1997), weather (Huesmann 1984), female body condition (Arnold et al. 1995), and nest parasitism (Brown and Brown 1981) could also influence nest survival.

### **3.4.3 Nest survival**

Brown (1981) reported a high nest success estimate (i.e., 68.4% Mayfield) over all four years of his study (i.e., 1977 - 1980). My Mayfield nest success estimate was lower (~29.5%) but no 95% CI is available for historical data (P. Brown, IL Natural History Survey, pers. comm.) and further, my results may not be directly comparable because of methodological differences in nest searches. Nonetheless, nest success of scoters at Redberry Lake is generally higher than most other duck species (Klett et al. 1988, Sargeant and Raveling 1992), which may be an artifact of island nesting. Obtaining nest success estimates for scoters from mainland nesting habitats is difficult and ineffective because nests occur at very low densities. Scoters have a low renesting propensity because of their late nest initiations (Brown 1981, pers. obs.). This is important because species with relatively high renesting propensities can have high hen

success rates (i.e., proportion of females that hatch at least one egg) even though nest success may be low (Cowardin et al. 1985). For species with a low reneating propensity, nest success is equivalent to hen success (Sargeant and Raveling 1992). Thus, reneating propensity is an important determinant of the threshold level of nest survival that will sustain a population (Klett et al. 1988). Given that (1) population growth rate is equivalent to the sum of adult survival probability and recruitment rate (i.e., assuming no immigration/emigration) and (2) populations change through time, then changes in recruitment can have important consequences for population change if adult survival probability is high (Nichols and Hines 2002, Williams et al. 2002). Thus, populations of ducks that nest early with a proclivity to reneat require a lower threshold of nest survival rate than comparative species of ducks that nest later with lower reneating potential, given comparable adult survival. For populations of scoters to persist, a high nest success relative to other duck species may be required because of other scoter life history traits (i.e., low duckling and first year survival probabilities and low reneating rate) (Brown 1981, unpubl. data).

Probability of daily nest survival was influenced by nest age. Survival of nests before onset of incubation had lower survival than nests in incubation stages (Klett and Johnson 1982). Predators may be acting on visual cues (i.e., exposed eggs or nest visitations by laying females) of the nest-site during early laying or during absence of the female (Klett and Johnson 1982). Lower survival probability of nests during laying may further be related to vulnerability of the nest-site, nest initiation date, and the behavior of the incubating female (see Klett and Johnson 1982). Nonetheless, effect of nest age may be confounded with that of temporal variation and individual heterogeneity (Dinsmore et al. 2002). I believe that temporal variation was not a problem because I found samples of nests throughout the nesting cycle (Dinsmore et al. 2002, unpubl. data). Individual heterogeneity (i.e., nests differing inherently in survival) may explain differences in nest survival (Dinsmore et al. 2002). My analyses suggested that failed nests were those with lower concealment, farther distance from edges, and closer to water.

Use of Program MARK to model daily nest survival enabled me to examine mechanistic processes of nest survival providing a more biologically meaningful

estimate of nest success (Dinsmore et al. 2002). Models with covariates outperformed unstructured models of simple nest success (i.e., from which the Mayfield estimate is derived). My modeling results were consistent with the concealment and distance to water hypotheses but not the distance to edge hypothesis (Filliater et al. 1994); nests closer to the edge tended to have higher survival rates. Studies have found gadwall nests closer to habitat edges have higher success rates (Pasitschniak-Arts et al. 1998, Clark and Shutler 1999). My results are not directly comparable to these studies; however, because nesting habitat on islands within Redberry Lake are comprised of native field habitat with plant species mixed together, with no anthropogenic influences such as agricultural activity (i.e., fragmentation). Thus, my measure of edge is fine scale as opposed to patch level (i.e., planted dense nesting cover) of these other studies and the only “real” edge, at the landscape level, may be the water surrounding the island(s) (see Stephens et al. *in press* for review).

### **3.5 CONCLUSION**

For scoters nesting at Redberry Lake late nest initiation date and a longer incubation period may be contributing to a decrease in nest survival by increasing the duration of exposure to predators. Furthermore, the abundance of predators on islands that historically had no mammalian predators may help to explain the presumable decrease in nest success. However, lower values of nest success may be acceptable if adult survival probability is sufficiently high.

Even though nest concealment is frequently cited as the most important factor influencing nest survival (Crabtree et al. 1989, Martin 1992), our understanding of factors determining nest survival and nest-site selection is limited. Numerous interacting abiotic and biotic factors have profound impacts on nest-sites and incubating females. Nevertheless, I obtained clear evidence that scoters favor well-concealed sites, located close to edges, farther from water, and on islands where nesting females and nests are better protected. Further, since early-laying is the time of highest nest mortality, concealed nest-sites are necessary to protect nests (1) because the protracted egg laying period (1 egg/ 1.5 days for scoters) renders nests unattended for long periods of time and (2) high ambient temperatures can reduce egg viability (Arnold 1993).

Importantly, fitness for individuals adaptively selecting nest-sites seasonally early may be high; earlier nesting females (i.e., have larger clutches) are thought to have higher nesting success (Flint and Grand 1996) and higher offspring survival (Guyn and Clark 1999) and thus contribute a higher proportion of recruits to the local population (Dzus and Clark 1998, Blums et al. 2002). Lastly, I encourage use of more biologically meaningful models to improve estimation of DSR because it provides a more valuable estimate of nest survival through modeling of pertinent biological covariates (e.g., weather conditions, female condition, habitat variables).

#### **4. SURVIVAL OF WHITE-WINGED SCOTER DUCKLINGS: CONSEQUENCES OF MATERNAL, DUCKLING, AND ECOLOGICAL TRAITS**

##### **4.1 INTRODUCTION**

Despite its potential influence on recruitment, offspring survival in free-ranging ducks has received limited study because of difficulties in obtaining estimates (Johnson et al. 1992). Advances in technology, theory (Lebreton et al. 1992), and numerical methods with associated software (White and Burnham 1999) for estimation of vital rates in free-ranging animals now enable researchers to draw inferences about the interplay of ecological covariates and offspring survival. However, these developments are relatively recent, and few studies have quantified the ecological effects frequently hypothesized to influence survival probabilities in ducklings (Guyn and Clark 1999, Gendron and Clark 2002). Using individually-marked adult females and ducklings, I investigated duckling and brood survival as a function of such factors.

Duckling survival is typically lowest during the first ten days after hatch in waterfowl, but usually stabilizes by 30 days after hatch (Mauser et al. 1994, Grand and Flint 1996, Guyn and Clark 1999). However, additional complexity in this general pattern might result from variation in chronology of nesting and physical attributes of nesting adults as well as their offspring. For example, ducklings that hatch relatively early within nesting seasons can have higher survival rates (Guyn and Clark 1999, Krapu et al. 2000, Pelayo and Clark *in press*), though this finding is not ubiquitous (Dawson and Clark 1996, Gendron and Clark 2002). Increasing abundance of seasonal food resources and improved habitat conditions, such as greater cover with emerging plant growth, may increase offspring survival probability (Rotella and Ratti 1992, Krapu et al. 2000). Still later in the nesting season, female vigilance can decline and abandonment of offspring may increase susceptibility of ducklings to (1) predation, (2)

inappropriate nutrition, and (3) thermal stress, reducing survival (Makepeace and Patterson 1980, Mendenhall and Milne 1985, Rotella and Ratti 1992, Grand and Flint 1996). However, social structure of broods may mediate such negative influences on duckling survival. For example, Kehoe (1989) and Blums et al. (2002) proposed that large brood size increases duckling survival, though results remain inconclusive (Dzus and Clark 1997, Guyn and Clark 1999, Gendron and Clark 2002). In addition, female traits such as structural size and body condition may influence duckling survival, perhaps by affecting ability to choose appropriate brood-rearing habitats to avoid predators, or physically defend offspring against predation attempts. Gendron and Clark (2002) found that gadwall (*Anas strepera*) ducklings had higher survival probabilities if accompanied by larger females in better nutritional condition. Body condition may be important because females endure energetic constraints during brood-rearing by defending broods and increasing vigilance for predators, ultimately decreasing time allocated for self maintenance (Bustnes and Erikstad 1991). Moreover, females in poor condition that results in decreased vigilance may show a proclivity to abandon broods (Eadie et al. 1988, Kehoe 1989), which in turn can suffer greater attrition immediately after abandonment (Bustnes and Erikstad 1991, Erikstad et al. 1993). This effect also can be highly variable across species or breeding range because some studies failed to demonstrate a connection between body mass of hens late in incubation and duckling survival probability (Arnold et al. 1995, Blums et al. 2002, Gendron and Clark 2002).

Duckling traits, such as size, body condition, and sex may also be important. Larger eggs produce structurally larger, better-conditioned ducklings (Anderson and Alisauskas 2001, Pelayo and Clark *in press*) with greater locomotor performance and perhaps superior thermoregulatory capacity as well as absolutely greater nutrient reserves (Anderson and Alisauskas 2002). Thus, ducklings from larger eggs have higher survival probabilities than those from smaller eggs (Dawson and Clark 1996, Christensen 1999, Pelayo and Clark *in press*). Sex differences in offspring survival have received little attention and might be predictable if food resources become limiting during growth. Cooch et al. (1997) found biased mortality of male lesser snow geese goslings (*Chen caerulescens*) during periods of food restrictions in the Arctic, which

may be because of sexually-size dimorphic young (i.e., males grow larger and faster). In more temperate latitudes, Korschgen et al. (1996) found male ducklings had higher survival rates relative to female canvasback (*Aythya valisineria*) ducklings whereas Dawson and Clark (1996) found that survival was independent of sex in lesser scaup (*Aythya affinis*) ducklings. Further, studies relating weather patterns and offspring survival are scarce. Adverse weather conditions (i.e., rainy, cold, and/or windy) can influence duckling survival rates directly, through hypothermia, or indirectly by inducing mortality through starvation, slowing growth rate, exposure, and increased activity levels or net energy loss (Korschgen et al. 1996, see Johnson et al. 1992). Blums et al. (2002) studied three species of duck and found the effect and importance of weather on duckling survival was species specific. Further, predation can be important during inclement weather; Bergman (1982) documented that adverse weather conditions can press broods into calm inlets where gull (*Larus spp.*) predation can be high. High winds can also decrease duckling survival by creating larger wave action or enhancing gull predation by increasing gull maneuverability (Gilchrist et al. 1998, Massaro et al. 2001).

Scoters on the large saline Redberry Lake are ideal subjects to test hypotheses about sources of variation in duckling survival. Large samples of nests are readily accessible on islands of Redberry Lake so ducklings can be marked “en masse”, broods are highly visible because emergent aquatic vegetation is absent, broods are subject to avian predation, and ducklings complete growth on the lake (Brown 1981, Kehoe 1989). My main objective was to estimate duckling survival in relation to maternal and duckling qualities as well as ecological variables. Specifically, I tested hypotheses about relationships between duckling survival and (1) hatch date, (2) initial brood size at hatch, (3) duckling size and body condition at hatch, (4) offspring sex, and (5) maternal female size and body condition at hatch. Further, I examined (6) the effect of weather on duckling survival. I assumed that duckling survival could be highly variable between years. Total brood loss often accounts for most offspring mortality (Talent et al. 1983, Orthmeyer and Ball 1990, Mauser et al. 1994); thus I considered survival probability from the standpoint of individual ducklings as well as entire broods.

## 4.2 METHODS

### 4.2.1 Capture and marking

Nest searches were conducted as described in chapter 3. Eggs were individually labeled with indelible ink and length (L) and width (W) were measured (nearest 0.1 mm with dial calipers) when final clutch size was attained. Egg size was obtained by using Hoyt's (1979) equation,  $\text{Volume (cm}^3\text{)} = 0.000507 * LW^2$ . Incubation stage was estimated by candling (Weller 1956). I then assumed incubation was 28 days, which allowed me to estimate hatch date for attempting to capture females at hatch.

Nests were visited just before or during hatch; duckling bills within pipped eggs were coded with an indelible marker for individual identification of ducklings, thereby linking them to their previously measured eggs. At or near hatch, incubating female scoters were either captured (1) by hand on the nest or (2) as they flushed from the nest using a hand-held net. Females were then weighed with a Pesola scale (nearest 10 g), measured (culmen, head length, and tarsal length were taken with dial calipers to nearest 0.1 mm), and given a standard U.S. Fish and Wildlife Service leg band and a uniquely colored nasal-marker (Lokemoen and Sharp 1985). Ducklings were captured at hatch on the nest, weighed (nearest 0.5 g), measured (culmen, head length, tarsus length to the nearest 0.01 mm), their sex determined through cloacal examination (in 2001 only), marked with a plasticine leg band (Blums et al. 1994, Blums et al. 1999), and given a uniquely colored nape-marker for individual identification (Gullion 1951, Pelayo and Clark *in press*). Nape-markers consisted of brass safety pins (size 00) and a 3-color plastic bead combination and were inserted through a loose pinch of skin at the base of each duckling's skull. Ducklings were then returned to nests from which they were initially removed and covered with nesting material. Initial brood size was calculated by subtracting number of eggs that did not hatch from final clutch size. Weather data obtained from a weather station at Redberry Lake included daily maximum, minimum and mean temperature, humidity, rainfall, and wind speed. All capture and marking procedures were approved by the University of Saskatchewan's Committee on Animal Care on behalf of the Canadian Council on Animal Care and the Canadian Wildlife Service issued federal access and scientific permits.

#### **4.2.2 Observation of marked females and ducklings**

To estimate duckling survival after hatch, I observed nasal-marked females and nape-marked ducklings on all days with no rain and low wind. Markers were read using 15-56x binoculars, 30-80x spotting scope, or a Questar telescope from a boat or shoreline when ducklings were most active (0700-1200 and 1600-2100 hrs). Identification of ducklings was accurate because of high visibility due to the lack of emergent vegetation (Brown and Fredrickson 1989). I monitored duckling survival for a 30-day period after hatch because survival rates are often constant thereafter (Orthmeyer and Ball 1990, Grand and Flint 1996, Guyn and Clark 1999). Use of individually marked ducklings and females enabled me to account for total brood mortality.

#### **4.2.3 Statistical analysis**

I tested whether brood size at hatch varied annually or with hatch date (PROC GLM, ANCOVA, SAS Institute 1989). I then standardized brood size at hatch for hatch date by using residuals from this analysis in all subsequent analyses. General linear models (PROC GLM, SAS Institute 1989) were used to test for annual differences in hatch dates.

Principal component analysis (PCA; PROC PRINCOMP, SAS Institute 1989) was used to derive a multivariate index to describe female and duckling body size, separately, based on the correlation matrix of tarsus, culmen, and head lengths (Rising and Somers 1989, Freeman and Jackson 1990). Duckling body mass was regressed (PROC GLM, SAS Institute 1989) on structural size and hatch date and residuals were used as an index of body condition (i.e., size-adjusted body mass) (Alisauskas and Ankney 1990, Hochachka and Smith 1991, Jakob et al. 1996). An index of female body condition was calculated by adjusting hatch weight with incubation stage, nest initiation date, and structural size; duckling body condition was calculated by adjusting weight (PROC GLM, SAS Institute 1989) with structural size and hatch date. All linear trends were confirmed by visual inspection of data plots.

Because weather data were only collected in 2001, I performed a separate analysis of duckling and brood survival and used PCA to describe weather conditions. A weather condition index was generated for each duckling for the first 7 days after

hatch. PCA of the correlation matrix resulted in a first principal component (PC1) with loadings of -0.50, 0.64, 0.58 for mean temperature (°C), mean humidity (mm) and mean maximum wind speed (km/h). Mean humidity was used rather than mean precipitation because there were numerous days with trace rainfall amounts (i.e., amounts are not different from zero). The first PC accounted for 69% of the summed variance of the 3 input variables, and explained slightly more variation than would occur by chance alone (61%) (Legendre and Legendre 1983, Jackson 1993). Thus, PC1 was used as a weather index. The second and third PC accounted for 23% and 8%, respectively and were not considered. Positive values of PC scores for PC1 corresponded to days that were colder, more humid, and windier than were days with negative values.

#### **4.2.4 Survival of ducklings**

Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) in Program MARK (White and Burnham 1999) were used to generate maximum likelihood estimates of apparent survival ( $\phi_i$ ) and recapture probability ( $p_i$ ) of marked ducklings during the first 30 days of brood-rearing. Assumptions of CJS model are: (1) marks are not lost, (2) marks are correctly recorded, (3) animals behave independently, (4) all individuals have similar survival and recapture probabilities, (5) all samples are instantaneous, and (6) losses through emigration from the population are permanent. Ducklings do not leave the lake before fledging (~ 8 weeks of age), so I assumed that apparent survival measured true duckling survival,  $S_i$ . Hence  $S_i$  was defined as the probability that a marked individual alive at age  $i$  survives until age  $i + 1$  and does not permanently emigrate. I defined recapture probability ( $p_i$ ) as the probability a marked individual alive at age  $i$  is seen. Initial encounter histories were 30 occasions ( $t_0$  to  $t_{29}$ ) but because data were sparse, leading to convergence problems during estimation, daily resightings were pooled into two-day intervals (2-day products of daily survival) resulting in 15 encounter occasions. I began analyzing duckling survival at  $t_0$  or at hatch. Because encounter histories were 15 occasions, the resulting survival estimate was only for 14 periods or 28-day survival. Consequently, I defined duckling survival as the probability of surviving to 28 days of age, while brood survival was defined as the probability of one duckling per brood surviving to 28 days of age.

I used the information theoretic approach based on Akaike's Information Criterion for model selection (Burnham and Anderson 1998). I developed a set of models based on biological hypotheses about offspring survival to thirty days, my main questions of interest (Burnham and Anderson 1998). The most parsimonious model was selected based on quasi-likelihood Akaike's Information Criterion (QAIC<sub>c</sub>) to correct for small sample size and lack of fit due to overdispersion (Akaike 1985, Burnham and Anderson 1998). Goodness-of-fit testing (GOF) determined if my global model  $\{S_{\text{year} \cdot a} p_{\text{year} \cdot a}\}$  sufficiently fit the data. I tested GOF on the global model, of my duckling level analysis, using a parametric bootstrap method in Program MARK. The variance inflation factor ( $\hat{c}$ ) was adjusted to account for lack of model fit (see Burnham and Anderson 1998). The adjusted  $\hat{c} = 1.26$  was calculated by dividing the deviance of the global duckling model by the mean deviance from 500 bootstrap iterations, while  $\hat{c}$  for the brood level analysis was 1.16. In the analyses of weather and sex effects on survival probability,  $\hat{c}$  was 1.31 and 1.19 for the duckling and brood level analyses, respectively. I used the logit link function to constrain parameters between 0 and 1 (White and Burnham 1999).

I used a 3-step approach to obtain my candidate model set, to reduce the total number of parameters in my models, and to reduce variance in estimates of survival and recapture probabilities (Lebreton et al. 1992). First, a global model included parameters that varied with duckling age. Models were reduced first with respect to constraints on recapture probability because it was the parameter of least interest, and then with constraints on survival probability. All combinations of age (i.e., age of ducklings since hatch) dependency were tested. Secondly, I fitted parameters to linear and quadratic trends with age by manipulating design matrices in Program MARK, giving parallel and differing slopes for each year on the logit scale. Finally, when the most parsimonious model was obtained without covariates, I estimated slopes between survival and individual-level covariates of interest by manipulating design matrices, giving parallel and differing slopes for covariates to survival for each year on the logit scale. Covariates were added to the most parsimonious model to consider additional structure and, subsequently, I estimated 95% CL ( $\hat{\beta}_1$ ). When the 95% CI ( $\hat{\beta}_1$ ) included zero, the precision of the estimate was considered low and it was removed from the model. I

then examined if model fit improved by reconsidering covariates that were judged to just include zero (e.g., -0.07 to 1.33) in the 95% CL ( $\hat{\beta}_1$ ), singularly and combined with other covariates. Analyses included  $n$  covariates such as hatch date, quadratic trend with hatch date, brood size, female condition, female size, duckling size, and duckling condition. I considered quadratic effect of hatch date on survival to examine if there was a cost to hatching very early or late. In addition, I used duckling sex and PC scores of weather as covariates in a separate analysis of 2001 data only. Duckling size, condition, and sex were not included in brood level analyses. Candidate models included additive and *a priori* two-way interactions only (i.e., hatch date \* duckling size, hatch date \* duckling condition). Covariates were standardized as  $(x_i - \bar{x})/SD$ . I used model weight ( $w$ ) to evaluate likelihood of each model. Model averaging, was used to weight estimates by  $w$  to draw inferences from the candidate model set to estimate bidaily survival rate (BDSR). Back transformation of slopes and intercepts was required to make predictions about

$S | x_1 \dots x_n$ , following

$$\hat{S}_i = \frac{1}{1 + e^{-(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \hat{\beta}_n x_n)}}$$

Estimates of  $\beta$ , for prediction purposes, were only used from the best approximating model. Asymptotic 95% CI was also calculated by back transforming from logit values estimated from upper and lower 95% CI of covariates. Unless otherwise indicated, tests were two-tailed with significance levels set at  $P < 0.05$ . All analyses were done using SAS (SAS Institute 1989) or Program MARK (White and Burnham 1999).

## 4.3 RESULTS

### 4.3.1 Marked individuals and brood size

I observed 35 and 59 nasal-marked females and 265 and 399 individually marked ducklings during 2000 and 2001, respectively. This resulted in 507 and 588 resightings of marked ducklings and 127 and 144 resightings of broods in 2000 and 2001, respectively. Hatching dates were similar between years: 20 July to 8 August, 2000 (median = 31 July), compared with 19 July to 10 August, 2001 (median = 30 July) ( $F =$

0.14,  $df = 1$ , 107,  $P = 0.75$ ). Initial brood sizes ranged from 1 to 13 ducklings each year, with similar average initial brood sizes in 2000 ( $\bar{x} = 7.6$ , 95% CI: 6.8 - 8.4,  $n = 35$ ) and 2001 ( $\bar{x} = 6.8$ , 95% CI: 6.3 - 7.4,  $n = 59$ ) ( $F = 1.44$ ,  $df = 2$ , 91,  $P = 0.23$ ), although brood size declined with later hatch dates ( $F = 15.49$ ,  $df = 1$ , 92,  $r^2 = 0.14$ ,  $P = 0.0002$ ; slope = -0.19, 95% CL: -0.10, -0.28).

### 4.3.2 Size variation of adult females and ducklings

Eigenvectors of PC1 from the correlation matrix of tarsus, culmen, and head lengths (0.52, 0.53, and 0.67 respectively) explained 61% of total variation in measurements made on adult females. Adult female body mass was positively correlated with PC1 ( $F = 16.22$ ,  $df = 1$ , 93,  $r^2 = 0.14$ ,  $P < 0.0001$ ), hence residuals from regression analysis were used as an index of female body condition. Mean female mass at hatch was 1102 g (95% CI: 1089 - 1115 g) and ranged from 950 to 1240 g.

Eigenvectors of PC1 from the correlation matrix of tarsus, culmen, and head lengths (0.57, 0.56, and 0.60, respectively) explained 60% of total variation in measurements made on ducklings. Residuals from regression were used as a body condition index for each duckling because body mass was positively correlated with PC1 ( $F = 102.35$ ,  $df = 1$ , 662,  $r^2 = 0.13$ ,  $P < 0.0001$ ). Duckling mass at hatch ranged from 39.0 to 63.0 g ( $\bar{x} = 52.5$  g, 95% CI: 52.2 - 52.8 g). Egg size was recorded for only 490 of 664 marked ducklings. Mean egg size was 72.7 cm<sup>3</sup> (95% CI: 72.3 - 73.1 cm<sup>3</sup>) and ranged from 57.2 to 83.6 cm<sup>3</sup>. Larger eggs produced structurally larger ( $F = 105.57$ ,  $df = 1$ , 488,  $r^2 = 0.18$ ,  $P \leq 0.0001$ ; slope = 1.43, 95% CI: 1.15 - 1.70), heavier ( $F = 744.84$ ,  $df = 1$ , 488,  $r^2 = 0.60$ ,  $P \leq 0.0001$ ; slope = 0.86, 95% CI: 0.80 - 0.92), and better-conditioned ducklings ( $F = 377.73$ ,  $df = 1$ , 488,  $r^2 = 0.44$ ,  $P \leq 0.0001$ ; slope = 0.79, 95% CI: 0.71 - 0.87). Duckling sex was determined only in 2001; there were 196 male and 203 female ducklings, respectively (49:51, M:F sex ratio). Male ducklings were structurally larger ( $F = 29.46$ ,  $df = 1$ , 397,  $P \leq 0.0001$ ), in slightly poorer condition ( $F = 3.92$ ,  $df = 1$ , 397,  $P = 0.048$ ), and had similar body masses ( $F = 0.08$ ,  $df = 1$ , 397,  $P = 0.77$ ) relative to female ducklings; there was no difference in egg size between the sexes ( $F = 1.89$ ,  $df = 1$ , 271,  $P = 0.17$ ).

### 4.3.3 Survival and recapture probabilities of ducklings and broods

Duckling survival in 2000 was only 0.016 (95% CL: 0.001, 0.031) while in 2001 it was 0.021 (95% CL: 0.000, 0.042). Brood survival was 0.084 (95% CL: -0.036, 0.200) in 2000 and 0.138 (95% CL: -0.007, 0.283) in 2001. Bidaily survival probability of ducklings for the first 14 days of age was slightly lower in 2001 than in 2000 (Fig. 4.1) but was higher from day 17 to 28 of age in 2001 (Fig. 4.1). Duckling mortality was greatest during the first 2 days after hatch in both years and it was estimated as 0.537 and 0.653 of all losses during 2000 and 2001, respectively (Fig. 4.2). Furthermore, 0.80 and 0.92 of duckling losses occurred during the first 6 days after hatching in 2000 and 2001, respectively (Fig. 4.2). Resighting probability was similar between years but differed markedly from age 14 to 19 (Fig. 4.3). Mean recapture rates of ducklings were 0.39 in 2000 and 0.44 in 2001, respectively. Mean recapture rates of broods were 0.43 and 0.45 in 2000 and 2001, respectively. Brood observations in October suggested that nape-marked ducklings of known age fledged at about 8 weeks of age.

### 4.3.4 Correlates of duckling and brood survival

Model selection based on QAIC<sub>c</sub> indicated that duckling survival in 2000 was a function of a quadratic trend with age ( $\hat{\beta}_{A^2} = -0.04$ , 95% CL: -0.06, -0.01), hatch date ( $\hat{\beta}_{HD} = -0.63$ , 95% CL: -0.87, -0.40), initial brood size ( $\hat{\beta}_{BS} = 0.32$ , 95% CL: 0.12, 0.54) (Fig. 4.4), as well as an interaction between hatch date and duckling condition ( $\hat{\beta}_{HD \times DC} = -0.33$ , 95% CL: -0.55, -0.11); thus, survival probability of ducklings in better condition was higher throughout the season relative to ducklings in poorer nutritional condition (Table 4.1). In 2001, duckling survival displayed a linear trend with age ( $\hat{\beta}_A = 0.29$ , 95% CL: 0.14, 0.44), in addition to a quadratic relationship with hatch date ( $\hat{\beta}_{HD^2} = -0.23$ , 95% CL: -0.41, -0.04), and simple positive relationships with initial brood size ( $\hat{\beta}_{BS} = 0.68$ , 95% CL: 0.42, 0.93) (Fig. 4.4), and female size ( $\hat{\beta}_{FS} = 0.21$ , 95% CL: -0.02, 0.44), but negative relationships with female condition ( $\hat{\beta}_{FC} = -0.30$ , 95% CL: -0.51, -0.08); finally, a weak interaction between hatch date and duckling size ( $\hat{\beta}_{HD \times DS} =$

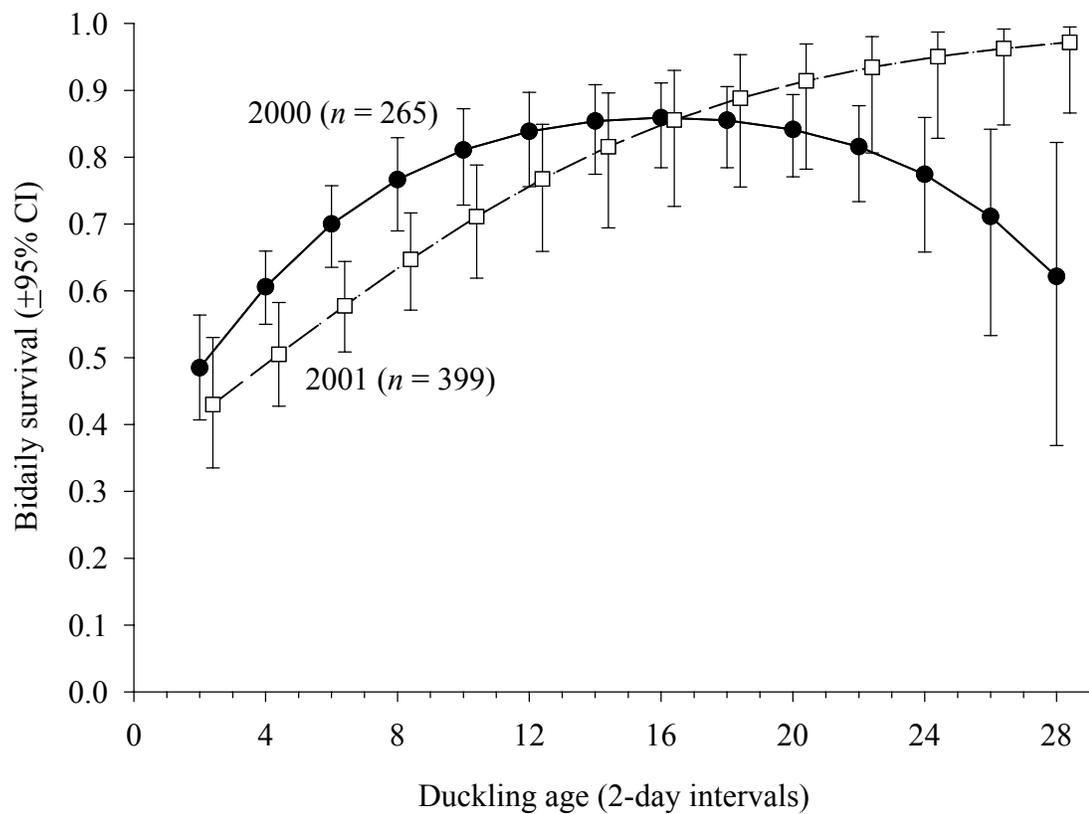


Figure 4.1. Estimates of 2-day (bidaily) survival rates for white-winged scoter ducklings in relation to their age (days) at Redberry Lake, Saskatchewan, 2000-2001. Estimates were calculated using weighted averages based on a candidate model set. The averages were weighted according to QAIC<sub>c</sub> values from each model.

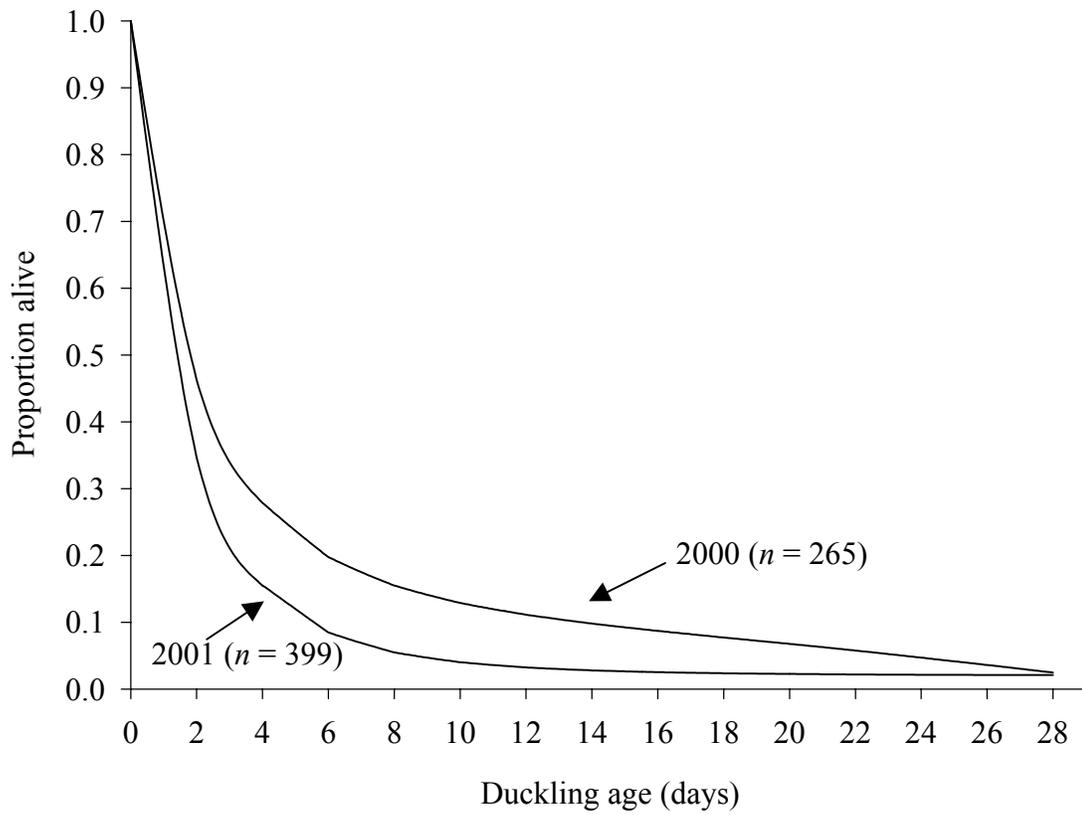


Figure 4.2. Proportion of white-winged scoter ducklings surviving by age at Redberry Lake, Saskatchewan, 2000-2001.

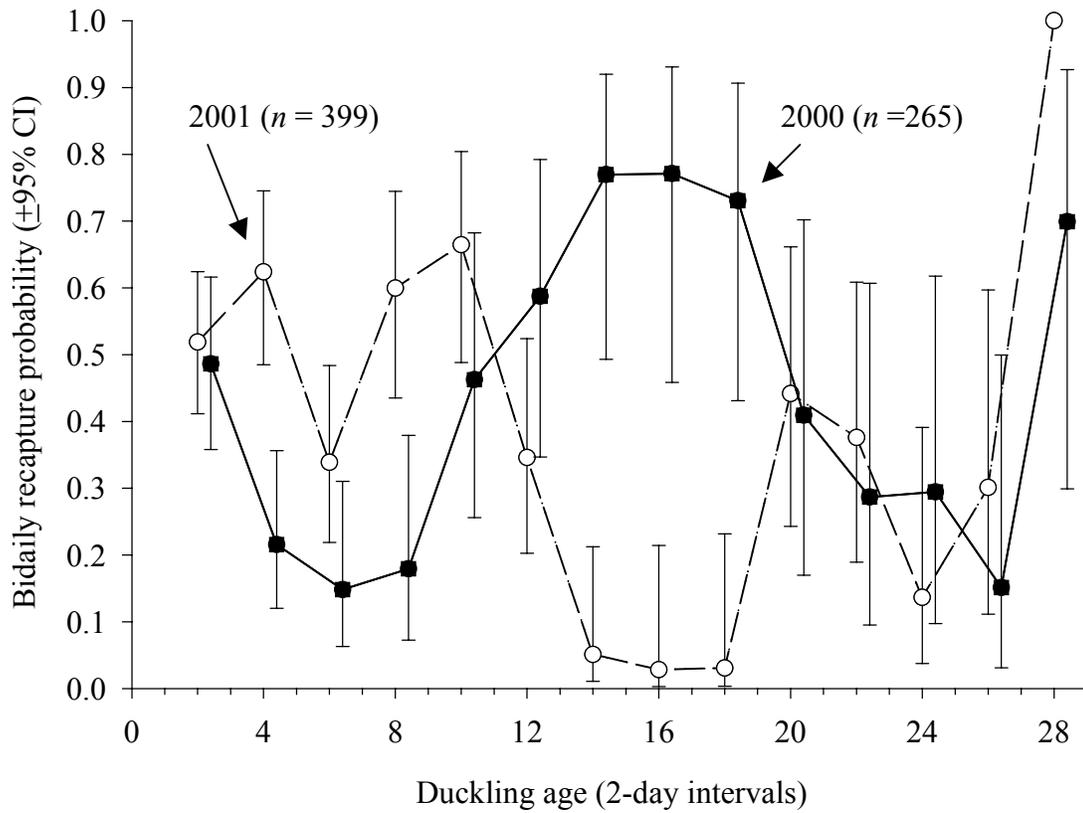


Figure 4.3. Estimates of 2-day (bidaily) recapture probabilities of white-winged scoter ducklings in relation to their age at Redberry Lake, Saskatchewan, 2000-2001. Estimates were calculated using weighted averages based on a candidate model set. The averages were weighted according to QAIC<sub>c</sub> values from each model.

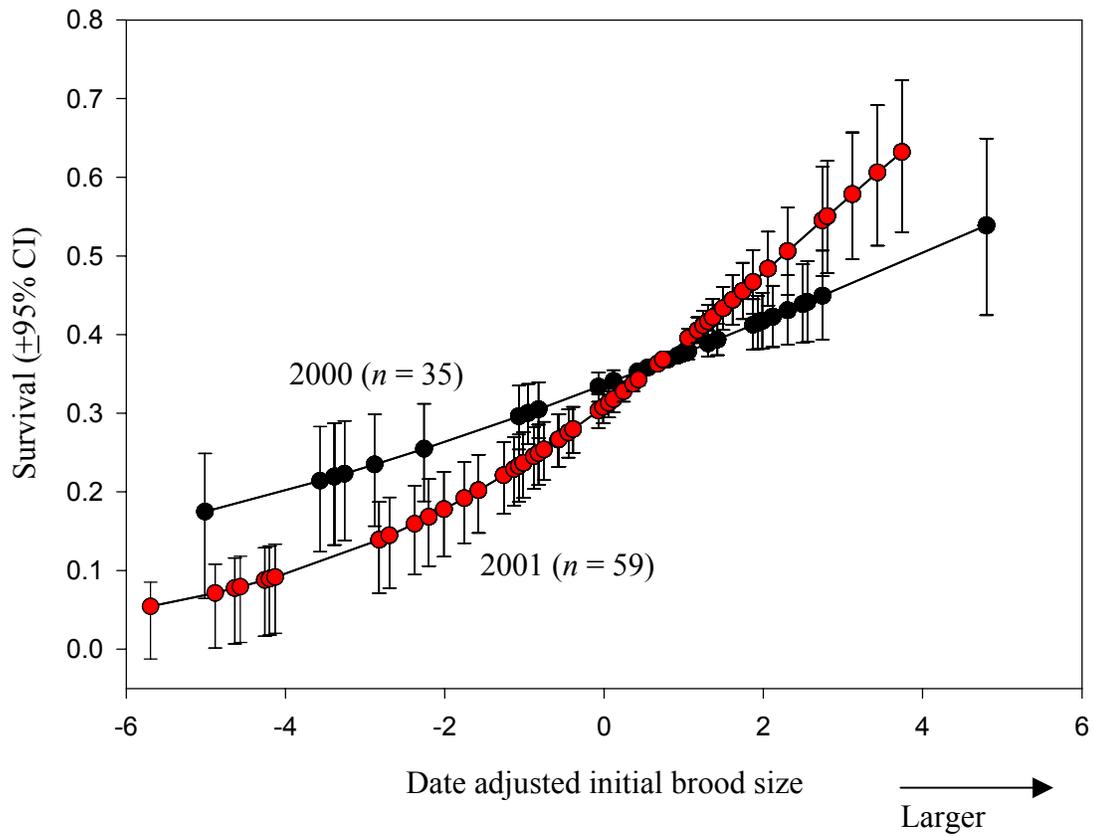


Figure 4.4. Relationship between white-winged scoter duckling survival and initial brood size at hatch (date corrected residuals) at Redberry Lake, Saskatchewan in 2000 and 2001, respectively.

Table 4.1. Model selection for estimation of survival,  $S$ , and recapture probability,  $p$ , of white-winged scoter ducklings on Redberry Lake, Saskatchewan, 2000-2001. Only 11 of 40 models, those with  $\Delta \text{QAICc} \leq 10$  are considered here, ranked by ascending  $\Delta \text{QAICc}$ . The variance inflation factor is 1.26.

Model <sup>a</sup>	QAICc <sup>b</sup>	$\Delta \text{QAICc}^c$	$w_i^d$	K <sup>e</sup>	Deviance <sup>f</sup>
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{fs}01+\text{hd}^*\text{dc}00+\text{hd}^*\text{ds}01} p_{\text{year}^*a}\}$	1779.65	0	0.150	40	1696.57
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{fs}01+\text{hd}^*\text{dc}00} p_{\text{year}^*a}\}$	1780.35	0.70	0.106	40	1697.27
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{fs}01+\text{ds}01+\text{hd}^*\text{dc}00} p_{\text{year}^*a}\}$	1780.35	0.70	0.106	41	1695.11
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{ds}01+\text{hd}^*\text{dc}00} p_{\text{year}^*a}\}$	1780.43	0.78	0.102	40	1697.34
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{fs}01+\text{hd}^*\text{dc}00} p_{\text{year}^*a}\}$	1780.50	0.85	0.098	39	1699.57
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{ds}01+\text{hd}^*\text{dc}00} p_{\text{year}^*a}\}$	1780.53	0.88	0.097	39	1699.60
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{hd}^*\text{dc}00+\text{hd}^*\text{ds}01} p_{\text{year}^*a}\}$	1780.67	1.02	0.090	39	1699.74
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{dc}00+\text{fc}01+\text{fs}01+\text{ds}01+\text{hd}^*\text{dc}00+\text{hd}^*\text{ds}01} p_{\text{year}^*a}\}$	1780.83	1.18	0.083	42	1693.43
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fs}+\text{fc}01+\text{ds}01+\text{hd}^*\text{dc}00+\text{hd}^*\text{ds}01} p_{\text{year}^*a}\}$	1781.09	1.44	0.073	42	1693.69
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fs}+\text{dc}00+\text{fc}01+\text{ds}01+\text{hd}^*\text{dc}00+\text{hd}^*\text{ds}01} p_{\text{year}^*a}\}$	1781.81	2.16	0.051	43	1692.24
$\{S_{\text{year}^*A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}01+\text{hd}^*\text{dc}00} p_{\text{year}^*a}\}$	1782.13	2.48	0.043	38	1703.35

<sup>a</sup> Model factors included year effects (00 = 2000, 01 = 2001, and year), duckling age dependency (a), linear trend with age (A), quadratic trend with age ( $A+A^2$ ), constant daily survival (.), hatch date (hd), quadratic hatch date ( $\text{hd} + \text{hd}^2$ ), initial brood size (bs), female condition (fc), female size (fs), duckling condition (dc), duckling size (ds), hatch date \* duckling condition ( $\text{hd}^*\text{dc}$ ), and hatch date \* duckling size ( $\text{hd}^*\text{ds}$ ).

Table 4.1 continued

<sup>b</sup> Quasi-likelihood Akaike's Information Criterion with small sample correction.

<sup>c</sup> Difference in QAIC<sub>c</sub> values between the model with the lowest QAIC<sub>c</sub> value.

<sup>d</sup> Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

<sup>e</sup> Number of estimable parameters.

<sup>f</sup> Deviance is difference between  $-2\log$ -likelihood of the current model and that of the saturated model.

0.24, 95% CL: -0.04, 0.53) suggested that larger ducklings had higher survival probability if they hatched earlier and the strength of the relationship increased as the season progressed (Table 4.1). Female size and the interaction between hatch date and duckling size just included zero. There was no relationship between female condition and hatch date or initial brood size ( $P$ 's  $\geq 0.40$ ) suggesting that females in better condition at hatch did not nest earlier or have larger brood sizes at hatch. Recapture probability was best modeled to include age dependency among years (i.e., year \* age). In 2000, brood survival was a function of a quadratic trend with age ( $\hat{\beta}_{A^2} = -0.02$ , 95% CL: -0.03, -0.01) and in 2001 a linear trend with age ( $\hat{\beta}_A = 0.21$ , 95% CL: 0.02, 0.40). Survival probability was a quadratic function of hatch date ( $\hat{\beta}_{HD^2} = -0.29$ , 95% CL: -0.58, -0.01) and simple function of initial brood size ( $\hat{\beta}_{BS} = 0.86$ , 95% CL: 0.48, 1.25) in both years (Table 4.2). Recapture probability varied by age in 2000, but was constant in 2001.

The best model from the candidate set that considered effects of weather and duckling sex on survival, was structured such that duckling survival showed a linear trend with age ( $\hat{\beta}_A = 0.31$ , 95% CL: 0.16, 0.45), and was related to initial brood size ( $\hat{\beta}_{BS} = 0.57$ , 95% CL: 0.31, 0.82), female condition ( $\hat{\beta}_{FC} = -0.22$ , 95% CL: -0.44, 0.00), duckling condition ( $\hat{\beta}_{DC} = 0.18$ , 95% CL: -0.04, 0.40), duckling size ( $\hat{\beta}_{DS} = 0.24$ , 95% CL: 0.00, 0.47), and negatively related to poor weather ( $\hat{\beta}_{PC1} = -0.70$ , 95% CL: -0.97, -0.43) (Fig. 4.5); an interaction between hatch date and duckling size ( $\hat{\beta}_{HD \times DS} = 0.21$ , 95% CL: -0.07, 0.50) suggested that larger ducklings had higher survival probability if they hatched later, but the effect was much weaker in smaller ducklings (Table 4.3). The 95%CL for  $\hat{\beta}_{HD \times DS}$ ,  $\hat{\beta}_{FC}$ , and  $\hat{\beta}_{DC}$  just included zero. There was no evidence that duckling sex was important to survival ( $\hat{\beta}_S = 0.01$ , 95% CL: -0.22, 0.24). Recapture probability was best modeled to include age dependency.

Table 4.2. Model selection for estimation of survival,  $S$ , and recapture probability,  $p$ , of white-winged scoter broods on Redberry Lake, Saskatchewan, 2000-2001. Only 5 of 32 models, those with  $\Delta \text{QAICc} \leq 10$  are considered here, ranked by ascending  $\Delta \text{QAICc}$ . The variance inflation factor is 1.16.

Model <sup>a</sup>	QAICc <sup>b</sup>	$\Delta \text{QAICc}^c$	$w_i^d$	K <sup>e</sup>	Deviance <sup>f</sup>
{ $S_{\text{year}+A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}} p_{00a_{01}}$ }	647.80	0	0.47	21	601.94
{ $S_{\text{year}+A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fs}} p_{00a_{01}}$ }	648.99	1.19	0.26	22	600.74
{ $S_{\text{year}+A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}} p_{00a_{01}}$ }	650.06	2.25	0.15	22	601.80
{ $S_{\text{year}+A+A^2_{00}+\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}+\text{fs}} p_{00a_{01}}$ }	651.35	3.55	0.08	23	600.70
{ $S_{\text{year}+A+A^2_{00}+\text{year}*\text{hd}+\text{hd}^2_{01}+\text{bs}+\text{fc}+\text{fs}} p_{00a_{01}}$ }	653.67	5.87	0.02	28	590.60

<sup>a</sup> Model factors included year effects (00 = 2000, 01 = 2001, and year), brood age dependency (a), linear trend with age (A), quadratic trend with age ( $A+A^2$ ), constant daily survival (.), hatch date (hd), quadratic hatch date ( $\text{hd} + \text{hd}^2$ ), initial brood size (bs), female condition (fc), female size (fs).

<sup>b</sup> Quasi-likelihood Akaike's Information Criterion with small sample correction.

<sup>c</sup> Difference in QAIC<sub>c</sub> values between the model with the lowest QAIC<sub>c</sub> value.

<sup>d</sup> Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

<sup>e</sup> Number of estimable parameters.

<sup>f</sup> Deviance is difference between  $-2\log$ -likelihood of the current model and that of the saturated model.

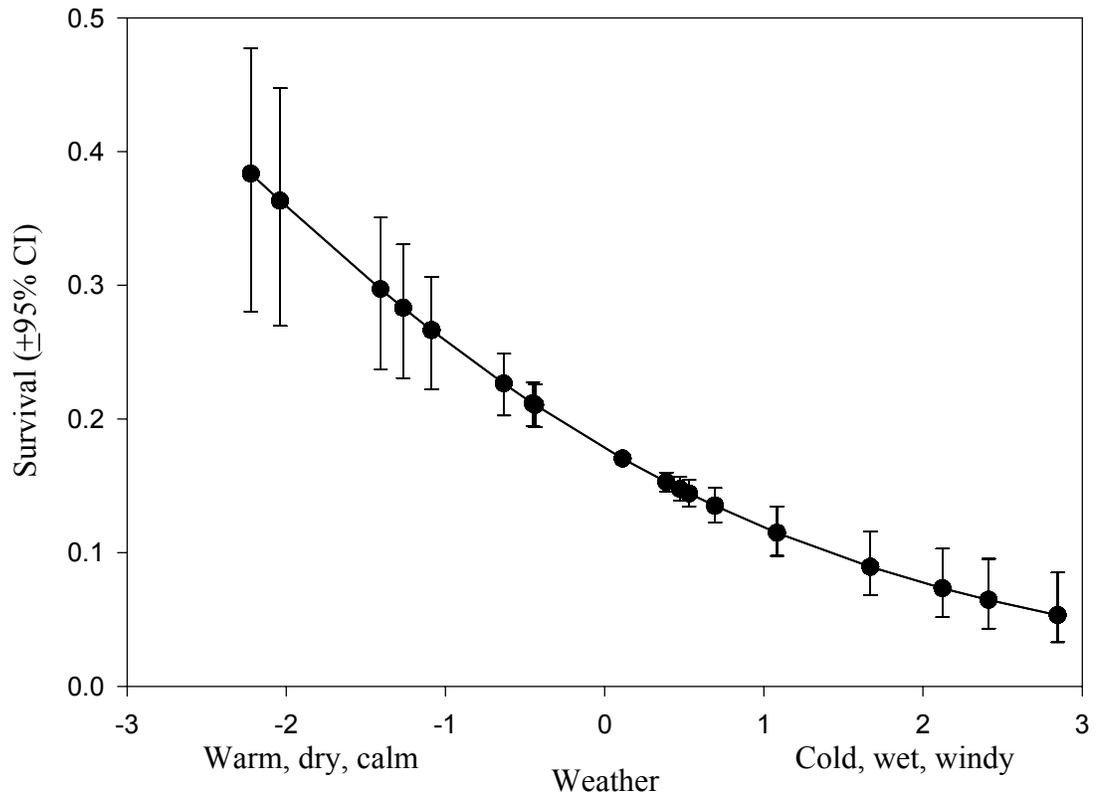


Figure 4.5. Relationship between white-winged scoter duckling survival and weather during the first week after hatch at Redberry Lake, Saskatchewan. The weather condition index was generated using principal component analysis in 2001 only.

Table 4.3. Model selection for estimation of survival,  $S$ , and recapture probability,  $p$ , of white-winged scoter ducklings on Redberry Lake, Saskatchewan, 2001. Only 15 of 23 models, those with  $\Delta \text{QAICc} \leq 10$  are considered here, ranked by ascending  $\Delta \text{QAICc}$ . The variance inflation factor is 1.31.

Model <sup>a</sup>	QAICc <sup>b</sup>	$\Delta \text{QAICc}^c$	$w_i^d$	K <sup>e</sup>	Deviance <sup>f</sup>
$\{S_{A+bs+fc+dc+ds+pc1+hd*ds} p_a\}$	733.46	0	0.166	22	687.64
$\{S_{A+bs+fc+dc+ds+pc1} p_a\}$	733.47	0.01	0.165	21	689.81
$\{S_{A+bs+fc+ds+pc1} p_a\}$	733.69	0.23	0.148	20	692.19
$\{S_{A+bs+fc+ds+pc1+hd*ds} p_a\}$	734.02	0.55	0.126	21	690.36
$\{S_{A+bs+dc+ds+pc1} p_a\}$	734.99	1.52	0.077	20	693.48
$\{S_{A+bs+dc+ds+pc1+hd*ds} p_a\}$	735.15	1.68	0.071	21	691.49
$\{S_{A+bs+fc+pc1+hd*ds} p_a\}$	735.44	1.98	0.061	20	693.94
$\{S_{A+bs+ds+pc1} p_a\}$	736.37	2.91	0.038	19	697.02
$\{S_{A+bs+fc+pc1} p_a\}$	736.65	3.18	0.033	19	697.29
$\{S_{A+bs+ds+pc1+hd*ds} p_a\}$	737.00	3.54	0.028	20	695.50
$\{S_{A+bs+fc+dc+pc1} p_a\}$	737.25	3.79	0.025	20	695.75
$\{S_{A+bs+dc+pc1+hd*ds} p_a\}$	737.48	4.02	0.022	20	695.98
$\{S_{A+bs+pc1+hd*ds} p_a\}$	738.48	5.02	0.013	19	699.13
$\{S_{A+bs+dc+pc1} p_a\}$	739.06	5.59	0.010	19	699.70
$\{S_{A+bs+pc1} p_a\}$	739.29	5.83	0.009	18	702.08

<sup>a</sup> Model factors included duckling age dependency (a), linear trend with age (A), initial brood size (bs), female condition (fc), duckling condition (dc), duckling size (ds), weather condition (pc1), and hatch date \* duckling size (hd\*ds).

<sup>b</sup> Quasi-likelihood Akaike's Information Criterion with small sample correction.

<sup>c</sup> Difference in QAIC<sub>c</sub> values between the model with the lowest QAIC<sub>c</sub> value.

<sup>d</sup> Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

<sup>e</sup> Number of estimable parameters.

<sup>f</sup> Deviance is difference between  $-2\log$ -likelihood of the current model and that of the saturated model.

Brood survival was a simple function of a linear trend with age ( $\hat{\beta}_A = 0.16$ , 95% CL: -0.02, 0.33), initial brood size ( $\hat{\beta}_{BS} = 0.87$ , 95% CL: 0.36, 1.40) and was negatively related to poor weather ( $\hat{\beta}_{PC1} = -0.47$ , 95% CL: -0.90, -0.05) (Table 4.4). Recapture probability for broods showed a linear trend with age ( $\hat{\beta}_A = 0.04$ , 95% CL: -0.05, 0.13).

## **4.4 DISCUSSION**

### **4.4.1 Duckling and brood survival**

My estimates of duckling and brood survival are the lowest published for ducks (see Grand and Flint 1996, Guyn and Clark 1999, Gendron and Clark 2002). Furthermore, estimates were lower than historic counts at Redberry Lake (Brown and Fredrickson 1989). Brown and Fredrickson (1989), based on comparison of known numbers of ducklings hatched and maximum number of ducklings in broods, stated that at least 0.66 (range of 0.60 to 0.72) of scoter ducklings died during the first 7 to 10 days after hatch. My estimates of duckling mortality were ~ 19 to 29% higher for the first 10 days after hatch (Fig. 4.2), although historic results are not directly comparable. Historically, ducklings were not individually marked (i.e., cannot account for total brood loss) and there was no estimate of detection probability (i.e., recapture rate) associated with the survival estimate. Nevertheless, mortality reported by Brown and Fredrickson (1989) was similar to those from other studies of scoters (i.e., consistently low) (Koskimies 1955, Hildén 1964, Mikola et al. 1994); these studies reported that, even in years of highest survival, 0.90 to 0.95 of all ducklings died. Lastly, duckling survival probability was higher for older ducklings (Grand and Flint 1996, Gendron and Clark 2002); most mortality occurred shortly after hatch (i.e., within 6 days) (Dzus and Clark 1997, Guyn and Clark 1999) with survival rates remaining relatively constant after 10 days of duckling age (Fig. 4.2). Compared with Brown's (1981) report of fledging at 10 weeks of age, my observations suggest that fledging occurs at 8 weeks.

### **4.4.2 Proximate cause of mortality**

Gull populations in the prairie parkland in Canada have grown ~ 11.4% since 1967 (Downes and Collins 2003). Further, there is a large gull population at Redberry

Table 4.4. Model selection for estimation of survival,  $S$ , and recapture probability,  $p$ , of white-winged scoter broods on Redberry Lake, Saskatchewan, 2001. Only 3 of 10 models, those with  $\Delta \text{QAICc} \leq 10$  are considered here ranked by ascending  $\Delta \text{QAICc}$ . The variance inflation factor is 1.19.

Model <sup>a</sup>	QAICc <sup>b</sup>	$\Delta \text{QAICc}^c$	$w_i^d$	K <sup>e</sup>	Deviance <sup>f</sup>
$\{S_{A+bs+pc1} p_A\}$	314.09	0	0.701	6	301.46
$\{S_{A+hd+hd^2+bs+fc+fs+pc1} p_A\}$	316.52	2.43	0.208	10	294.82
$\{S_{A+bs} p_A\}$	318.17	4.08	0.091	5	307.72

<sup>a</sup> Model factors included linear trend with age (A), hatch date (hd), a quadratic effect of hatch date ( $hd + hd^2$ ), initial brood size (bs), female condition (fc), female size (fs), and a weather condition index (pc1).

<sup>b</sup> Quasi-likelihood Akaike's Information Criterion with small sample correction.

<sup>c</sup> Difference in QAIC<sub>c</sub> values between the model with the lowest QAIC<sub>c</sub> value.

<sup>d</sup> Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

<sup>e</sup> Number of estimable parameters.

<sup>f</sup> Deviance is difference between  $-2\log$ -likelihood of the current model and that of the saturated model.

Lake (~ 13,000 nesting pairs) thus, predation rates on ducklings at the time of my observations may have increased. Gulls disperse from colonies to loaf on shorelines of islands around modal dates of scoter hatch, and appear to consume a high proportion of resident ducklings as ducklings enter the water with hens within a day of hatch (Brown and Brown 1981, Kehoe 1989, pers. obs.). Although scoter ducklings show specific adaptations, such as diving and crèching that may counter gull predation (Brown and Brown 1981), I suspect that high predation of scoter ducklings by nesting gulls overwhelms the potential for recruitment of locally produced scoters. Thus breeding islands currently may function as ecological traps (Dwernychuk and Boag 1972).

I assumed a negligible effect of markers on survival probability. Conceivably, nape-markers and plasticine leg bands may render ducklings more susceptible to predation events, decrease feeding efficiency, and/or indirectly predispose them to other forms of mortality. Blums et al. (1999) suggest that plasticine legbands do not increase mortality in any duck species. I could not devise a scheme to test for marker effects directly, although the percentage of marked ducklings did not change from < 2 days of age (46% of 385 ducklings observed) to ~ 28 days after hatch (39% of 72 ducklings observed,  $\chi^2 = 1.32$ ,  $df = 1$ ,  $P = 0.25$ ) suggesting no combined effect of either nape-tags or plasticine legbands.

#### **4.4.3 Factors influencing survival**

Duckling survival declined with advancing hatch date, and the severity of decline further depended on duckling size and condition. The declining pattern of survival with hatch date has been observed in other studies (Rotella and Ratti 1992, Dzus and Clark 1998) and may exist because of increased predation (Grand and Flint 1996), declines of wetland quality and food resources (Rotella and Ratti 1992, Sedinger and Raveling 1986, Cox et al. 1998), and decreased maternal care (Pöysä 1992) as the season advances. However, wetland quality may be less important to scoters because of their use of large permanent and saline lakes, such as Redberry Lake. Scoter ducklings fledge in early-October, so I believe that declining food resources (Brown and Fredrickson 1986), adverse weather conditions (lower minimum temperatures later in

the season) and perhaps increasing internal parasite loads and diseases (Bourgeois and Threlfall 1982) might reduce survival of ducklings hatched later.

Increased salinity levels can be fatal to young ducklings (Mitcham and Wobeser 1988). Salt glands may not function properly in neonates until after a week of exposure (Mitcham and Wobeser 1988, Stolley et al. 1999), even for species such as Common eiders (*Somateria mollissima*) (Devinck unpubl. data). Redberry Lake is saline and highest densities of broods often locate near freshwater sources (i.e., streams) and thus, access to freshwater after hatch may be crucial. Salinity may cause mortality directly, or indirectly through effects of weakened immune response and ability of ducklings to handle adverse weather and predation attempts (Swennen 1989). Further, elevated salinity levels may influence food availability (i.e., abundance of amphipods) for ducklings and may compromise the ability to assimilate nutrients and feed properly. Thus I hypothesize that salinity at Redberry Lake may play a role in reducing duckling survival by predisposing those that hatch there to inanition, internal parasitic loads, disease, weather, hypothermia, and predation events.

I found that likelihood of survival by scoter ducklings was related to social structure of broods. Small broods showed the lowest survival, although predators presumably should select larger broods to maximize foraging efficiency (Begon et al. 1996). I suspect that intense gull predation shortly after hatch makes large brood size adaptive (Kehoe 1989). Larger brood size may increase survival through (1) the dilution effect (i.e., larger brood size reduces the risk of predation per young) and (2) rapidly detecting and confusing predators (Eadie et al. 1988, Bustnes and Erikstad 1991, see Johnson et al. 1992). Accordingly, this adaptive pattern may have been significant in the evolution of a large clutch size. Adaptiveness of large brood size may include tradeoffs associated with large clutch sizes such as (1) longer exposure period of nests, which can decrease nest and female survival, (2) decreased egg viability, (3) reduced re-nesting propensity, and (4) decreased recruitment from later hatch dates (Dzus and Clark 1998, Chapter 4). Lastly, smaller broods may suffer higher mortality from reduced female attentiveness (e.g., decreased parental care because of higher parental self-maintenance) correlated with reduced investment and a relatively lower fitness value (Eadie et al. 1988, Dzus and Clark 1997).

Although scoter ducklings are believed to have a high tolerance to inclement weather (Koskimies and Lahti 1964), duckling survival showed a strong negative relationship with cold, wet, and windy weather. Ducklings likely require greater energy reserves to endure periods of severe weather, when there is a decrease in food intake and energy reserves are depleted (Johnson et al. 1992, Pelayo and Clark *in press*). Inclement weather can influence duckling survival rates directly, through hypothermia, or indirectly by inducing mortality through starvation, slowing growth rate, exposure, and increased activity levels or net energy loss (Johnson et al. 1992, Korschgen et al. 1996, Schmutz et al. 2001). High winds can also decrease duckling survival by improving maneuverability and success in attacks by foraging gulls (Gilchrist et al. 1998, Massaro et al. 2001). Interestingly, other studies did not detect consistent adverse effects of poor weather (Blums et al. 2002, Pelayo and Clark *in press*), but this may have been an artifact of my study site. Redberry Lake is about 10 km in diameter and high winds (i.e., 60 to 70 km/h) on such large lakes create severe wave action, increase exposure of ducklings to gulls, decrease feeding efficiency, and increase thermal stress through convective and conductive heat loss.

The importance of female condition and size were inconsistent throughout this study as it was in others (Arnold et al. 1995, Gendron and Clark 2002). I found that females in poorer condition had higher duckling survival. This result is contradictory to findings of Talent et al. (1983), which suggested that ducklings attended by poor conditioned females were more susceptible to predators and adverse weather conditions, although it is important to consider scoter ducklings are highly precocial and have a higher relative tolerance to inclement weather than other duck species (Koskimies and Lahti 1964). Observations suggest females that actively defend broods from gull attacks leave ducklings exposed while fending off gulls; in contrast passive females remained close to ducklings (pers. obs.). Ultimately, I hypothesize that this negative relationship between hen condition and ducklings survival resulted in part from poor condition females abandoning young after hatch; such ducklings often joined larger amalgamated broods in which probability of survival was higher relative to maternal broods (Kehoe 1989, unpubl. data).

Results from 2001 suggested a strong effect of duckling body size on subsequent duckling survival probability. Pelayo and Clark (*in press*) also found that ducklings hatching from larger eggs (i.e., larger, better-conditioned ducklings) had higher survival probabilities relative to those hatching from smaller eggs (Ankney 1980, Christensen 1999, Dawson and Clark 1996), though results remain inconsistent in other species (Smith et al. 1993, Williams et al. 1993). Further, Dawson and Clark (2000) found that ducklings hatching from larger eggs had a higher probability of recruitment into the local population. Larger offspring are thought to survive better than smaller individuals because they have (1) greater tolerance for lower ambient temperatures, (2) a lower surface area to volume ratio (i.e., can maintain homeothermy more efficiently), (3) better motor skills (i.e., performance), (4) larger yolk reserves, and (5) higher feeding efficiency (Rhymer 1988, Visser and Ricklefs 1995, Anderson and Alisauskas 2001, 2002). Moreover, in areas with large gull populations, larger, better-conditioned ducklings may survive because they have faster escape response and longer dive duration (Swennen 1989, Anderson and Alisauskas 2001). Ultimately, high mortality of small individuals may be related to small body size and lower energy reserves (i.e., poor condition) at hatch (Pelayo and Clark *in press*).

The influence of duckling size and condition on survival was confounded by an interaction between the effect of each covariate with hatch date. Specifically, ducklings in better condition and larger size survived better relative to poor conditioned and smaller ducklings, and this disparity increased as hatch dates progressed. Perhaps larger or better-conditioned ducklings are better able to survive as environmental conditions deteriorate later in the summer. For example, Anderson and Alisauskas (2001) found that larger King Eider ducklings show better locomotor performance than smaller ducklings. I believe that high predation pressure, adverse weather conditions, and high salinity levels may overwhelm the hypothesized benefits of factors such as female condition, female size, duckling condition, and duckling size on duckling survival. Finally, sex of ducklings, beyond sex-related differences in duckling size, was not important to survival (Cooch et al. 1997).

#### **4.5 CONCLUSION**

I set out to construct a parsimonious and empirically-derived model for survival of scoter ducklings. I failed to produce a parsimonious model because a large number of my predictions were supported by data; thus probability of survival by scoter ducklings at Redberry Lake is a demonstrably complex function of a variety of biotic and abiotic factors. My models which include interactions between extrinsic factors (i.e., unpredictable inclement weather and hatching date) and intrinsic factors (i.e., physical and nutritional traits of individual hens and ducklings and brood sizes) predict probabilities of duckling survival that are lower than any previously reported. External factors are thought to be more important than intrinsic factors because they generally have more influence on offspring survival and recruitment (Blums et al. 2002). The magnitude of such effects likely vary from year to year and may result in “boom or bust” recruitment by this population of scoters. Because of large numbers of nesting gulls and subsequent high predation on young ducklings as they leave island nests, my results are consistent with an ecological trap; suggesting very low potential for recruitment based on observations of 0.11 28-day old duckling produced/nesting female. For scoters, a relatively low reproductive success may be adequate to sustain local populations because of high adult survival, although current findings suggest high adult survival may not compensate for low recruitment potential.

## 5. SYNTHESIS

Little was known about causes or mechanisms of population decline in scoters. Declines have left breeding populations virtually extinct from the prairies, northward range retraction continuing in the parklands, and significant declines are also occurring in the boreal forest of Canada (Trost 1998). Population decline may result from changes in any component(s) of the life cycle (Figure 1.3). Therefore, all vital rates require estimation for a complete understanding of the relative contributions of separate life cycle components to population change. High annual adult survival probability of about 0.77 (Krementz et al. 1997) suggests that population declines resulted from low recruitment, specifically inadequate nesting success and offspring survival (Brown and Brown 1981, Brown and Fredrickson 1989). I focused on estimating nesting success and offspring survival in scoters, two components of recruitment, and specifically tried to identify ecological factors that influence these components. I also estimated these vital rates for a comparison with previously reported estimates to understand if prescriptions for conservation of scoters may have changed.

Nest-site selection was similar to historic accounts at Redberry Lake. Scoters chose well-concealed sites, located close to edges, far from water, and on islands where nesting females and nests are better protected; nest-site selection complemented other life history attributes; scoters nest later than other waterfowl species, have a large clutch size, and experience high energetic demands during incubation. Thus, nesting strategies that rely on decreased nest detection or accessibility by predators (Martin 1995) should be adaptive. Further, concealment of nests should be advantageous because (1) early-laying is the time of highest nest mortality, (2) protracted egg laying period renders nests unattended for long periods of time, and (3) high ambient temperatures can cause unattended eggs to become inviable (Arnold 1993).

Nest success at Redberry Lake may have decreased by ~ 30% since the 1970s and 1980s, which may be due to access of generalist predators to breeding islands.

Changes in quality of nesting habitat in Canada, with the advent of increasing human development of breeding lakes and agriculture, has caused large-scale landscape changes that likely are important factors leading to decreased nesting success (Turner et al. 1987). As native parkland and grassland are converted to agricultural lands, female survival and nest success on mainland nesting areas decline because of increased abundance and foraging efficiency of generalist predators (Krasowski and Nudds 1986, Turner et al. 1987). Other aspects of scoter nesting ecology at Redberry Lake also have changed from historic estimates. For example, scoter nest initiations were slightly later than historic estimates (Brown 1981) and, in addition, mean hatch dates for successful nests were markedly later (i.e., average of 7 days) than they were historically. Because there was no long term change in clutch size and scoters rely on exogenous reserves to lay eggs, scoters at Redberry Lake are incubating ~ 3 days longer than historically. This could impinge on female fitness in at least three ways; (1) nest success of females in poor condition may be compromised because of decreased nest attentiveness, (2) breeding season survival could decline because nesting females are exposed to predation pressure for longer periods and (3) later hatch could reduce duckling survival.

Estimates of survival, whether for ducklings or broods, are the lowest of published studies and the first for white-winged scoter broods in North America. I suspect that intense gull predation shortly after hatch had the largest influence on duckling survival. Elevated gull populations due to increased agricultural activities and landfills may adversely influence recruitment of ducklings into the breeding population from this island-nesting population by decreasing duckling survival. At Redberry Lake, gull chicks fledge around mid-July and gull colonies disperse to loaf on shorelines of islands during scoter hatch appearing to consume a high proportion of resident ducklings as they enter the water. Most mortality occurred during the first six days after hatch. Variation in both duckling and brood survival were best modeled with effects of hatch date, initial brood size, and weather; survival probability clearly declined with advancing hatch date, increased with larger initial brood sizes, and increased with favorable weather conditions. Nevertheless, unpredictable adverse weather events, coupled with intense gull predation, seasonal decline in food resources, decreased hen vigilance, and elevated salinity levels on brood rearing areas all may reduce duckling

survival and increase in importance during years of later hatch (Brown 1981, Mendenhall and Milne 1985, Mitcham and Wobesor 1988, Erikstad et al. 1993).

For populations of scoters to persist, a high nest success relative to other duck species may be required to compensate for low duckling survival, low renesting rate, and possibly low first-year survival probabilities (Brown 1981, Traylor unpubl. data). Low offspring survival (e.g., ~ 0.016 over 28 days) coupled with declines in nest success rate (i.e., ~ 0.30 Mayfield) likely are the most important causes of local population decline at Redberry Lake. However, further work on other components of the life cycle such as adult survival, breeding propensity, and juvenile/subadult survival are needed to fully understand the population dynamics of this species.

This study has provided estimates of nesting success and duckling survival at the southern extent of the retracted breeding range of scoters. These estimates may not be representative across the predominant breeding range of scoters (e.g., boreal forest of Northern Canada), although conducting studies in the boreal forest is logistically and financially challenging. Studies currently underway in the boreal, to examine scoter breeding ecology, are experiencing difficulty locating nests, which ultimately hampers our ability to assess duckling survival and obtain reliable estimates (i.e., poor sample sizes). Nevertheless, it is important that studies in the core breeding areas of the boreal continue to take place and with the advent of new technologies and increased awareness of population declines more studies will begin to address these concerns. Ultimately, these studies will give much needed comparisons to my findings.

There are several new areas that need to be addressed to examine scoter population decline. Although intense predation on nests and ducklings is evident from my research at Redberry Lake, some of the ecological effects on components of scoter recruitment may be linked to events during spring migration or on previous winter areas. Identification of wintering/migration areas of individual females breeding at Redberry Lake and associated levels of contaminants and nutritional resources may provide further insights on reduced breeding success and survival of nests and ducklings. Secondly, other components of the life cycle need to be estimated. Problems in estimation of adult survival, juvenile/subadult survival, and breeding propensity exist because of difficulties following individuals from fledging to breeding

and marking large numbers of birds for long periods of time. Collecting information on these vital rates would improve our knowledge of scoter population dynamics. Thirdly, on the local scale at Redberry Lake, because scoters are initiating nesting later and clearly hatching later it would be interesting to explain why. Information on incubation constancy may provide clues about mechanisms behind what appears to be protracted incubation duration by scoters compared to historical estimates. Conversely, reduced incubation constancy would suggest that scoters might be returning in poorer nutritional condition (i.e., less body reserves, which are accumulated before arrival on breeding areas). Brown and Fredrickson (1987) and Dobush (1986) suggest exogenous (i.e., dietary) reserves are used for laying and incubation while endogenous (i.e., body) reserves are used to satisfy daily energy demands during incubation. Since there was no long-term change in clutch size, depleted body reserves require that scoters take more frequent breaks from incubation, and thus increase incubation duration. Ultimately, research concerning nutritional condition of arriving and prelaying female scoters, in comparison to historical estimates, may give insight regarding contemporary breeding success and its importance to current population declines and further, underscore the importance of wintering/migrational ground effects to declines. Fourth, the role of increased salinity levels on food resources and subsequent duckling survival remains unclear. Redberry Lake likely has increased in salinity as water levels continue to decline, but to my knowledge no one has quantified the effects on the lake ecosystem and on duckling ecology. Fifth, the role of gull predation across the breeding range of scoters on the prairies and parklands need to be ascertained. Is gull predation really important in the boreal forest or is it limited to the southern extent of the breeding range? Are other factors more important such as weather or hatch date? Finally, a comprehensive population model for scoters at Redberry Lake should be developed using existing estimates of life cycle components to evaluate the impacts of varying vital rates on population growth. Research on these key areas should lead to greater understanding of causal factors for population decline over a wider area. Nevertheless, my research suggest that conservation actions in the parkland might focus most productively on enhancing parameters of recruitment, instead on managing for increased adult survival.

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