

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

JOSHUA J. TRAYLOR,^{1,4} RAY T. ALISAUSKAS,^{1,2} AND F. PATRICK KEHOE³

¹Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada;

²Prairie and Northern Wildlife Research Center, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada; and

³Ducks Unlimited Canada, No. 200 10720-178 Street, Edmonton, Alberta T5S 1J3, Canada

ABSTRACT.—Population surveys indicate a trend of declining abundance of scoters (*Melanitta* spp.) in North America. Little is known about changes in life-history traits that may be responsible for the recent population decline of White-winged Scoters (*Melanitta fusca deglandi*). Therefore, we studied nesting ecology of White-winged Scoters at Redberry Lake, Saskatchewan, during the summers of 2000–2001. We found 198 nests and examined nest-site selection by comparing habitat features of successful nests, depredated nests, and random sites. Discriminant function analysis differentiated habitat features—measured at hatch—of successful nests, depredated nests, and random sites; lateral ($r = 0.66$) and overhead ($r = 0.35$) concealment were microhabitat variables most correlated with canonical discriminant functions. We also modeled daily survival rate 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. Nest survival increased throughout the laying period and stabilized during incubation, and showed positive relationships with nest concealment and distance to water and a negative relationship with distance to edge. Considering those factors, a model-averaged estimate of nest survival was 0.24 (95% CL: 0.09, 0.42). We concluded that White-winged Scoters selected nesting habitat adaptively, because (1) successful sites were more concealed than depredated sites; (2) nest sites (both successful and depredated) had higher concealment than random sites; and (3) nest sites were on islands, where success is greater than on the mainland. Received 27 February 2003, accepted 30 March 2004.

RESUMEN.—Los censos poblacionales de *Melanitta* spp. indican una tendencia decreciente de su abundancia en Norte América. Actualmente se sabe muy poco sobre los cambios en los rasgos de historia de vida que pueden ser responsables de esta reciente disminución poblacional en *Melanitta fusca deglandi*. Por esta razón estudiamos la ecología de nidificación de *M. fusca deglandi* en el Lago Redberry, Saskatchewan, durante los veranos de 2000 y 2001. Encontramos 198 nidos y examinamos la selección de sitio de nidificación, comparando las características de los hábitats de nidos exitosos, nidos depredados y sitios distribuidos al azar. Un análisis de función discriminante diferenció las características de hábitat—medidas en el momento de eclosión—de nidos exitosos, nidos depredados y sitios al azar. Las coberturas lateral ($r = 0.66$) y superior ($r = 0.35$) de los nidos fueron las variables de microhábitat más correlacionadas con las funciones canónicas discriminantes. También modelamos la tasa de supervivencia diaria de los nidos en función del año, las tendencias lineales y cuadráticas de la edad del nido, la fecha de inicio del nido y siete variables de microhábitat. La supervivencia de nidos, estimada con un modelo de tiempo constante (i.e. estimación del éxito de nidificación de Mayfield) fue 0.35 (95% LC: 0.27, 0.43). Las estimaciones del éxito de nidificación fueron menores que aquellas medidas en el Lago Redberry durante los años setenta y ochenta. La supervivencia de nidos fue aumentando durante el período de puesta y se estabilizó durante la incubación, y mostró una relación positiva con la cobertura del nido y la distancia al agua, y una relación negativa con la distancia al borde. Considerando estos factores, una estimación de la supervivencia de los nidos basada en un promedio de los modelos fue de 0.24 (95% LC: 0.09, 0.42). Concluimos que *M. fusca deglandi* seleccionó los sitios de nidificación de una manera adaptativa debido a que (1) los sitios exitosos estaban más ocultos que los sitios depredados; (2) los sitios de nidificación (i.e. exitosos y depredados) estuvieron más ocultos que los sitios al azar; y (3) los nidos se encontraron en islas donde el éxito fue mayor que en el continente.

⁴Present address: Prairie and Northern Wildlife Research Center, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada. E-mail: joshua.traylor@ec.gc.ca

NEST SURVIVAL, A critical component of recruitment (Johnson et al. 1992), can be affected by predation, weather, female body condition, and nest-site placement (Afton and Paulus 1992, Johnson et al. 1992, Flint and Grand 1996). Predation is the most important proximate cause of nest failure in birds (Martin 1995). Birds often adopt strategies to reduce predation risk, including (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 population numbers may enable the birds to 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 vegetative characteristics, such as density. Tall, dense vegetation may confer protection by creating visual barriers, increasing numbers of available nesting sites, and hindering movement of mammalian predators (Livezey 1981, Martin 1993). Nest success can also 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 factors responsible for the recent population decline (Sea Duck Joint Venture Management Board unpubl. data) of White-winged Scoters (*Melanitta fusca deglandi*; hereafter "scoters"). As part of an effort to begin to understand scoter population biology, we set out to estimate survival and recruitment and determine the contribution of each to local population change. Here, we focus on recruitment only, because reliable estimates of survival using mark-recapture (Lebreton et al. 1992) require several years of work. Our first objective was to estimate nest initiation dates, clutch sizes,

egg hatchability, and hatch dates for scoter nests. Second, to understand patterns of nest use and ongoing natural selection, we compared characteristics of successful nests, depredated nests, and randomly located sites (Clark and Shutler 1999). Third, we estimated nest survival and compared current estimates to historical estimates from our study site. We also investigated the importance of microhabitat at nest sites and nest initiation date to daily survival rate (DSR) of nests; examination of microhabitat features among successful and depredated nests in areas with high depredation rates can facilitate understanding of the process of nest-site selection (Clark and Shutler 1999). We predicted that (1) earlier nesting; (2) higher concealment (lateral, overhead, or both); (3) denser and taller vegetation; (4) greater distance from habitat edges; and (5) greater distance from water would be positive correlates of DSRs.

STUDY AREA AND METHODS

Fieldwork was conducted on Redberry Lake, Saskatchewan (52°43'N, 107°09'W), ~100 km northwest of Saskatoon, Saskatchewan, from June to August in 2000 and 2001 (Fig. 1). Redberry Lake is a 4,500-ha federal bird sanctuary and World Biosphere Reserve that supports the largest known local breeding population of scoters in North America (F. P. Kehoe unpubl. data). Previous nesting studies of scoters at Redberry Lake were done during 1975–1980 (Brown 1977, 1981) and 1984–1985 (Kehoe 1986). The lake is within aspen parkland habitat characterized by rolling hills, numerous small wetlands, and small-grain agriculture (Brown 1981). Most scoters nest on Gull Island (51 ha), Pelican Island (50 ha), New Tern Island (3 ha), and Old Tern peninsula (6 ha) (Fig. 1). Dominant island and peninsula vegetation consists of grasses (*Poacea* spp.), northern gooseberry (*Ribes oxycanthoides*), rose (*Rosa* spp.), western snowberry (*Symphoricarpos occidentalis*), Saskatoon berry (*Amelanchier alnifolia*), willow (*Salix* spp.), thorny buffaloberry (*Shepherdia argentea*), silverberry (*Elaeagnus commutata*), and trembling aspen (*Populus tremuloides*). California (*Larus californicus*) and Ring-billed (*L. delawarensis*) gulls inhabit New Tern Island and the north point of Pelican Island. Coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), Great Horned Owls (*Bubo virginianus*), Red-tailed Hawks (*Buteo jamaicensis*), American Crows (*Corvus brachyrhynchos*), and Black-billed Magpies (*Pica hudsonia*) use all the islands (J. J. Traylor pers. obs.). Further descriptions of the study area are given by Brown (1981) and Kehoe (1986).

Nest searches.—We conducted nest searches on three islands and on portions of mainland near the eastern and western lake shores from early June to

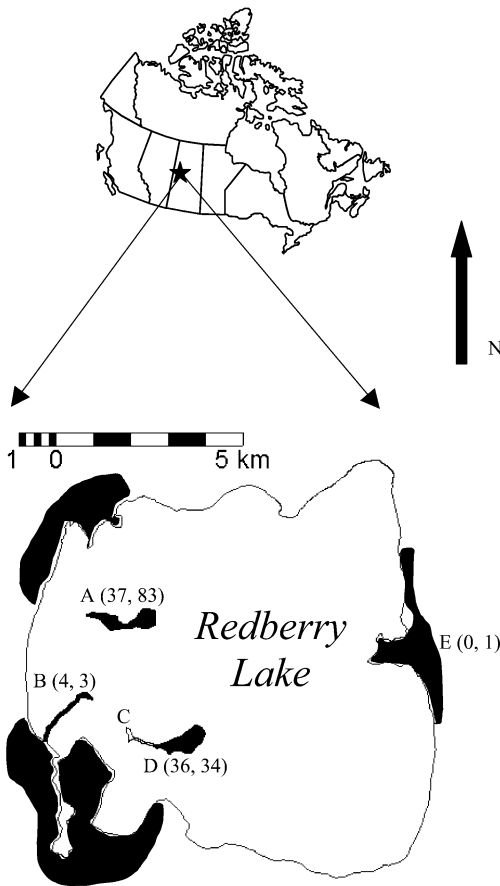


FIG. 1. Redberry Lake federal bird sanctuary and Biosphere Reserve, Saskatchewan. Letters within the lake indicate (A) Gull Island, (B) Old Tern Peninsula, (C) New Tern Island, (D) Pelican Island, and (E) mainland. Numbers in parentheses are number of nests located in 2000 and 2001, respectively. Shaded areas indicate islands and mainland areas searched for nests.

mid-August, 2000–2001 (Fig. 1). No nest searching or other research activities occurred on New Tern Island, where an American White Pelican (*Pelecanus erythrorhynchos*) colony was located. We performed nest searches between 0700 and 2200 hours. All island and mainland habitats in the study were systematically searched on foot five times and three times per year, respectively. A nest was defined as a bowl containing at least one egg. When we found a nest, we recorded its position using a global positioning system (GPS) to aid in relocation; we then covered eggs with nesting material to simulate natural incubation recesses by females (Götmark 1992). Clutch size (i.e. number of eggs deposited) was recorded only

for nests that successfully hatched. Nest initiation dates were estimated by subtracting stage of embryonic development (obtained by candling eggs; Weller 1956) and clutch size (assuming that 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). We visited nests every 7–10 days to determine fate (i.e. successful, abandoned, depredated, or unknown); visitation intervals were changed so that nests were visited at the estimated hatch date (Flint and Grand 1996). We considered nests successful if at least one egg hatched, as indicated by presence of egg membranes (Klett et al. 1988) or ducklings. We considered nests depredated if there was evidence of visitation by mammalian predators (e.g. presence of guard hair, nest bowl dug out, teeth marks in egg shell, no yolk on shell) or avian predators (e.g. presence of feathers, beak marks on shell, yolk in or on shell). We considered nests abandoned if no new eggs were deposited during laying or if eggs remained cold, uncovered, or both. Otherwise, we classified nest fate as “unknown.”

We assumed that observer effects (i.e. human-induced abandonment) 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. Olson and Rohwer (1998) reasoned that repeated visits to nests might cause decreased success rates through indirect factors associated with human disturbance (Krasowski and Nudds 1986, Rotella et al. 2000). Because of differences in frequency and timing of nest searches, historical nest-success estimates from the 1970s and 1980s may not be directly comparable to ours. We 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 during 1977–1980 and began searches between 25 June and 20 July each year; our data suggested that, because a disproportionate number of nests were depredated at the early laying stage, Brown may have missed a substantial number of depredated nests; thus, his estimates may have been biased high. Therefore, we urge caution when comparing current and historical estimates of nest success.

Nest microhabitat.—We measured seven microhabitat variables each year, within a 1-m² quadrat centered on the nest and random sites. Maximum live- and dead-vegetation heights were measured separately, directly over the nest, with a meter stick (nearest centimeter). We measured height of both live and dead vegetation because we predicted that dead plants could provide primary cover when nests were initiated and that live vegetation, as it grew, would provide additional cover. Vegetation density was taken as number of stems per meter squared within the quadrat. Overhead concealment (%) was an index

taken 1 m directly above nests by inserting a black cardboard disc with five 6.5-cm² squares into the nest bowl and estimating the average percentage of each white square that was visible from 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 visible in each cardinal direction; a concealment score was then computed as a mean value from each direction (Brua 1999). We estimated distance to nearest edge (meters), using a meter stick, to the nearest point where a visible change in plant community was judged to occur (e.g. opening, shrub patch)—a finer-grained measure than that used by Clark and Shutler (1999). We measured distance in meters to nearest water directly, by counting 1-m paces.

Random sites.—Distances and cardinal directions from nests of random locations 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 was the distance (meters) from nest. That approach for selecting random plots was reasonable, because scoters nested throughout all island habitats, and the maximum distance of a nest from water was ~200 m. At each location, the researcher threw a rock over his or her shoulder to determine the random site (Clark and Shutler 1999). New points were selected when a random site occurred in water or on sand, because scoter nests were never found at such sites (J. J. Traylor pers. obs.).

Statistical analyses.—We used general linear models (PROC GLM; SAS Institute 1989) to test for annual differences in nest initiation dates, clutch sizes, egg hatchability, and hatch dates. We used linear regression to estimate changes in clutch size and egg hatchability with advancing nest initiation date. We confirmed all linear trends 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. For analysis of nest-site selection, we excluded all abandoned nests and used successful and depredated nests only. We assessed habitat variables for normality by examining skewness and kurtosis, plotting data, and assessing Shapiro-Wilks test statistics (PROC UNIVARIATE; SAS Institute 1989). Maximum height of live and dead vegetation, 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 original data were orthogonal, so we used all seven nest-site variables in a discriminant function analysis (DFA). We used DFA to determine characteristics that best discriminated between successful nests, depredated nests, and random sites (Krasowski and Nudds 1986, Brua 1999, Clark and Shutler 1999).

When performing DFA, we were interested only in examining habitat differences between groups. Therefore, we tested for yearly and seasonal differences in habitat characteristics before combining data for both years, after finding no interaction between habitat characteristics and year or season. To control for seasonal influences on the seven nest-site variables, we 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, we created z scores (standard normal deviates) within years for residuals of each vegetation variable, thus controlling for year effects (Clark and Shutler 1999).

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

We used an information-theoretic approach for model selection (Burnham and Anderson 1998). We used the logit-link function to force all estimates of DSR to the interval (0, 1) (Lebreton et al. 1992). Akaike's Information Criterion (adjusted for sample size, AIC_c ; Akaike 1973) was used to select the best approximating model(s). Currently, there is no goodness-of-fit test for nest survival data in MARK (Dinsmore et al. 2002). 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, we considered models without covariates where DSR showed temporal trends over the nesting cycle (i.e. with nest age). We assessed temporal variation in nest age by comparing fit of models with DSR that (1) was constant over the 49-day nesting cycle, $\{S_t\}$; (2) was constant over the 49-day nesting cycle in each year (i.e. testing annual differences, $\{S_{year}\}$); (3) showed a linear trend over the nesting cycle, $\{S_t\}$; or (4) included a quadratic trend over the nesting cycle to accommodate some nonlinearity, $\{S_{Age,2}\}$ (Dinsmore et al. 2002). We did not want to over-fit the data, so we 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 $\{S_{A+2}\}$. First, we considered fit of DSR to linear $\{S_{A+A^2+NID}\}$ and quadratic $\{S_{A+A^2+NID+NID^2}\}$ trends in nest initiation date. Then we considered all seven nest-habitat variables—height of live vegetation (L), height of dead vegetation (D), overhead concealment (OC), lateral concealment (LC), vegetation density (VD), distance to edge (E), and distance to water (W)—as covariates to the most parsimonious model at that stage, $\{S_{A+A^2+NID+L+D+OC+LC+VD+E+W}\}$. If the 95% CL of $\hat{\beta}_1$ for a covariate on the logit scale included zero, we concluded lack of effect and removed it from the model. Finally, we examined whether model fit would improve by reconsidering covariates that only just included zero (e.g. -0.07 to 1.33) in the 95% CL of $\hat{\beta}_1$, singularly and combined. Only additive models without interactions were considered. We used model weight (w_i) to evaluate likelihood of each model; w_i are normalized Akaike weights and indicate relative support for different models in the candidate model set, and can be interpreted as the evidence that a model is the most appropriate, given the data and model set (Burnham and Anderson 1998). To accommodate model uncertainty, we used model-averaged estimates from the candidate model set to draw inferences about variation in DSR (Burnham and Anderson 1998).

All covariates were standardized in 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 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 (Chicago, Illinois), SAS (1989), or MARK (White and Burnham 1999).

RESULTS

Nesting ecology.—We found 77 nests in 2000 and 121 nests in 2001 (Table 1); all but 1 were on islands (Fig. 1). Females were seen flying to locations in mainland habitat, but we 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^{-1} in 2000 and 2001, respectively; whereas nest densities for area searched on the mainland (~ 900 ha) were 0 and ~ 0 nests ha^{-1} 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 1). There were no differences between years in nest initiation dates ($F = 1.88$, $df = 1$ and 185 , $P = 0.17$) or hatch dates ($\bar{x} = 30$ July, 95% CL: 29, 31 July) ($F = 0.14$, $df = 1$ and 107 , $P = 0.75$; Table 1). Mean clutch size was

8.8 (95% CL: 8.6, 9.1; Table 1) and was similar between years ($F = 3.32$, $df = 1$ and 138 , $P = 0.07$), but declined by 0.11 (95% CL: 0.08, 0.14) eggs day^{-1} during the nesting season ($F = 40.44$, $df = 1$ and 138 , $r^2 = 0.23$, $P \leq 0.0001$). Mean egg hatchability was 84.5% (95% CL: 80.8, 88.2%), with no annual change ($F = 0.00$, $df = 1$ and 107 , $P = 0.99$) (Table 1). Egg hatchability declined by 1.1% day^{-1} (95% CL: 0.5, 1.7) during the nesting season ($F = 11.46$, $df = 1$ and 107 , $r^2 = 0.10$, $P \leq 0.0001$).

Nest-site selection.—Scoters nested predominantly in northern gooseberry. Rose, grasses, Saskatoon bushes, wild mustard (*Brassica kaber*), and western snowberry, or a combination of those species, were present less frequently than northern gooseberry within quadrats centered on the nest. Discriminant function analysis revealed clear differences in habitat among sites (Wilks' λ , $U = 0.54$, $P < 0.0001$) and correctly classified 81.7% of successful nests, 12.2% of depredated nests, and 86.8% of random sites. A higher proportion of depredated nests were misclassified as successful nests than random sites (Fig. 2), though the overall correct classification rate was 71.0%, which was better than chance alone ($k = 0.50$, 95% CL: 0.41, 0.58, chance corrected, $z = 10.5$, $P < 0.0001$; Titus et al. 1984).

Because the first discriminant function explained 98.6% of variation in the data, we did not consider the second discriminant function. Lateral ($r = 0.66$) and overhead ($r = 0.35$) concealment were the original variables most strongly correlated with the first canonical discriminant function, producing the largest differences among groups (Table 2). Nests (both successful and depredated nests) had more lateral and overhead concealment than random sites, which strongly suggested nonrandom habitat selection (Fig. 2). Furthermore, depredated nests had $\sim 3\times$ less lateral and $\sim 2\times$ less overhead concealment than successful nest sites, which suggested strong selection against nests with low concealment (Fig. 2 and Table 2).

Nesting success.—We suspect that $\sim 9.6\%$ and $\sim 23.7\%$ of detected nests were depredated by avian predators in 2000 and 2001, respectively. Additionally, we estimated that roughly 17.8% and 8.8% of nests were depredated by mammalian predators and 12.3% and 9.6% were abandoned in 2000 and 2001, respectively; overall apparent nest success was 60.3% (44 of 73) and 57.0% (65 of 114) in 2000 and 2001,

TABLE 1. Number of nests found, mean initiation dates, mean clutch size, mean hatch date, mean egg hatchability (percentage of eggs that hatch per nest), and nesting interval length for White-winged Scoters at Redberry Lake, Saskatchewan, 1977–1980, 2000–2001. Historical 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 ^a	–	–	–	–	19 June (171) ^b	22 June (173)
95% CL	–	–	–	–	17–22 June	21–23 June
<i>n</i>	–	–	–	–	73	114
Nest initiation date ^c	13 June (164)	15 June (166)	17 June (168)	15 June (166)	18 June (170)	20 June (171)
95% CL	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% CL	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% CL	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
Egg hatchability (%)	81.3	83.9	72.0	89.1	84.5	84.5
95% CL	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 ^d	38	38	39	36	41	41
95% CL	36–40	36–40	37–41	35–37	39–43	39–43
<i>n</i>	73	70	102	71	44	65

^a Nest initiation date for successful and failed nests.
^b Julian date (164 = 13 June 2000 but 12 June 2001).
^c Nest initiation date for successful nests, for comparison with Brown's (1981) data.
^d Interval is the difference in days between mean initiation date and mean hatch date for successful nests.

TABLE 2. Nest-site variables for successful nests and depredated nests of White-winged Scoters and for random sites, and corresponding correlation coefficients with the canonical discriminant function for the first discriminant function. Bold values represent significant differences (no overlap of 95% CL) among the three groups.

Nest-site variable	Successful nests (<i>n</i> = 109) ^a	Depredated nests (<i>n</i> = 58)	Random sites (<i>n</i> = 167)	DFA correlation coefficient ^b
Live height (cm)	90.33 ± 7.42 ^c	82.39 ± 13.01	60.21 ± 5.50	–0.03
Dead height (cm)	46.74 ± 5.95	50.46 ± 9.59	34.08 ± 5.12	–0.30
Overhead concealment (%) ^d	20.64 ± 4.36	42.80 ± 8.26	68.59 ± 4.87	0.35
Lateral concealment (%) ^e	11.69 ± 2.65	32.90 ± 6.70	62.21 ± 5.11	0.66
Distance to edge (m)	1.03 ± 0.12	1.08 ± 0.18	1.56 ± 0.18	0.14
Distance to water (m)	113.44 ± 8.97	96.68 ± 13.99	106.9 ± 8.31	–0.06
Vegetation density (stems m ^{–2})	37.97 ± 3.67	32.79 ± 3.84	54.24 ± 8.04	0.05

^a Sample size.
^b Coefficients <|0.35| were deemed unimportant.
^c Mean ± 95% confidence limit.
^d Lower values for overhead concealment = more concealed.
^e Lower values for lateral concealment = more concealed.

respectively. Only one nest, in 2001, was classed as “unknown fate.”

In our comparison of candidate models, Mayfield nest success was 0.35 (95% CL: 0.27, 0.43) from model {S.}, which contains only an intercept term for DSR (Table 3). Mayfield nest success calculated for each year from model {S_{YEAR}} was 0.37 (95% CL: 0.25, 0.50) in 2000 and 0.34 (95% CL: 0.24, 0.43) in 2001,

which suggested that nest survival was similar between years. However, both of those simple models had poor performance when compared with more complex models in the candidate set. Our model-averaged estimate of nest survival was slightly lower at 0.24 (95% CL: 0.09, 0.42), which suggested that the simple Mayfield estimate could be biased by ~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). Daily nest survival increased throughout the laying period and was lower during the first 6 days than during days 11–13 of the nesting cycle (Fig. 3). Daily nest survival was higher throughout the first 28 days of incubation than during the first week of laying (Fig. 3). A model with DSR as a linear function of nest initiation date had stronger support than a model with DSR

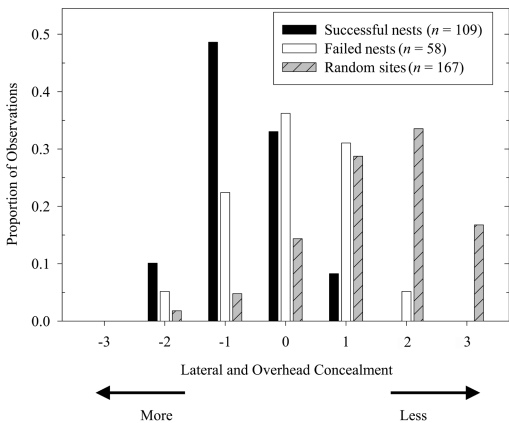


FIG. 2. Distribution of discriminant function scores for successful and depredated nests of White-winged Scoters and randomly located sites at Redberry Lake, Saskatchewan. Lateral and overhead concealment variables are listed (in order of importance) because loadings $\geq |0.35|$.

as a quadratic function of nest initiation date (Table 3). Daily survival rate of nests decreased with increasing nest initiation date (i.e. from $\{S_{A+A^2+NID}\}$. We estimated $\beta_{NID} = -0.21$, 95% CL: $-0.45, 0.03$, though the 95% confidence limit included zero.

When all covariates were added to model $\{S_{A+A^2}\}$, model quality improved by 14.5 AIC_c units (Table 3). Daily survival rate of nests from the most parsimonious model suggested that nest survival was a function of overhead concealment, lateral concealment, distance

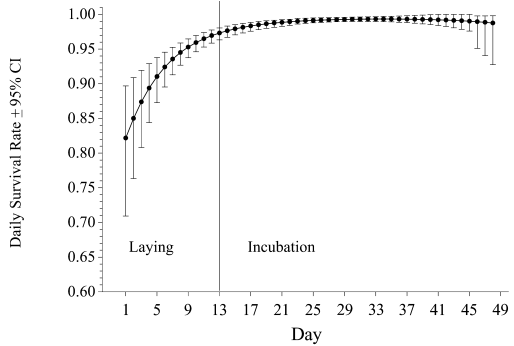


FIG. 3. Daily survival rate of White-winged Scoter nests during laying and incubation at Redberry Lake, Saskatchewan for 2000 ($n = 73$) and 2001 ($n = 114$), combined. Estimates $\pm 95\%$ CL were obtained using weighted averages based on a candidate model set and were weighted according to AIC_c values from each model.

TABLE 3. Summary of White-winged Scoter model-selection results of nest survival at Redberry Lake, Saskatchewan, 2000–2001, ranked by ascending ΔAIC_c .

Model ^a	Deviance ^b	K ^c	AIC _c ^d	ΔAIC_c ^e	w_i ^f
$\{S_{A+A^2+OC+LC+E+W}\}$	426.67	7	441.01	0.00	0.41
$\{S_{A+A^2+OC+E+W}\}$	429.62	6	441.88	0.87	0.26
$\{S_{A+A^2+OC+LC+W}\}$	430.25	6	442.51	1.49	0.19
$\{S_{A+A^2+OC+W}\}$	433.31	5	443.49	2.48	0.12
$\{S_{A+A^2+NID+L+D+OC+LC+VD+E+W}\}$	424.66	11	447.48	6.47	0.02
$\{S_{A+A^2+NID}\}$	453.04	4	461.16	20.15	0.00
$\{S_{A+A^2}\}$	455.93	3	462.01	20.99	0.00
$\{S_{A+A^2+NID+NID^2}\}$	452.78	5	462.96	21.95	0.00
$\{S_A\}$	465.12	2	469.15	28.14	0.00
$\{S_{\cdot}\}$	535.56	1	537.57	96.56	0.00
$\{S_{YEAR}\}$	535.31	2	539.35	98.33	0.00

^a Model factors included linear age trend (A), quadratic age trend (A+A²), constant daily survival (.), nest initiation date (NID), quadratic nest initiation date (NID + NID²), 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).
^b Deviance is difference between $-2\log$ -likelihood of the current model and that of the saturated model.
^c Number of estimable parameters.
^d Akaike's Information Criterion with small sample correction.
^e Difference in AIC_c values between each model and that with the lowest AIC_c value.
^f Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

to edge, and distance to water (Table 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 limits for $\hat{\beta}_{LC}$ and $\hat{\beta}_E$ included zero. Models with $\Delta AIC_c < 2$ had a cumulative weight of 86% (Table 3). There was limited support for importance of nest initiation date, maximum live and dead vegetation height, and vegetation density to nest survival (Table 3).

DISCUSSION

Nesting ecology.—Compared with historical values (Brown 1977, 1981), initiation dates and hatch dates for successful nests were later in our study (Table 1) and in 2002 (initiation date $\bar{x} = 18$ June, Julian date 169 and hatch date $\bar{x} = 29$ July; 95% CL: 27, 29 July, Julian date 210; interval length 41 days; C. Swoboda pers. comm.). Later hatch dates were a result not only of later nest initiation, but also of protracted nesting interval (Table 1). We 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 nutrients for egg formation (Dobush 1986). Clutch size was unchanged from historical levels, but the source of those 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, they may require more time before nesting to store nutrient reserves for incubation. Also, food availability at Redberry Lake may have declined because of changing lake dynamics, further impinging on scoters' ability to complete incubation. Lake water levels have dropped 10 m since 1940, and salinity levels (i.e. total dissolved solids 20.9 g L^{-1}) are approaching tolerance limits of amphipods (Hammer et al. 1990, Evans et al. 1996). *Gammarus* shrimp, once very abundant in the Redberry Lake ecosystem, are now thought to be rare, and perhaps extinct (Hammer et al. 1990). Furthermore, *Hyaella azteca*, the primary food of scoters at Redberry Lake and nearby lakes, may also have decreased in numbers

because of elevated salinity levels (Hammer et al. 1990) or low water levels. Lower water levels mean that some lakes (i.e. ≤ 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. Thus, protracted nesting intervals could have resulted from a combination of diminished daily rate of egg laying or prolonged incubation.

Delayed nesting and a 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, Traylor 2003). 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, J. J. Traylor 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 may increase in importance during years of later hatch (Mendenhall and Milne 1985, Erikstad et al. 1993).

Nest-site selection.—Our results suggest that nest concealment was the most important determinant of nest placement by scoters at Redberry Lake, and that survival was positively related to concealment. Our results were consistent with Brown (1977, 1981) 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, whereas 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 2). 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).

Our study sheds 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: 197 nests were found on islands, but 1 was found on mainland habitats, which were far greater in area than the searched parts of islands (Fig. 1). We believe that comparison was valid, because habitat was similar between islands and mainlands and detection probability of active nests by observers should have been similar. Nest survival is generally higher for ducks on islands than on mainland areas (Lokemoen and Woodward 1992, Clark and Shutler 1999).

Our results are consistent with those of some studies that suggested that nest concealment was the most important factor discriminating between successful and depredated nests (Crabtree et al. 1989, Martin 1992), though that is not always the case (Clark and Shutler 1999). We 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 depredated nests (Martin 1993, Clark and Shutler 1999). Accordingly, as with birds in general, persistence of adaptive nest-placement by scoters is likely 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 of safe habitats by females (Pulliam 1988, Clark and Shutler 1999).

Nesting cover that provides high concealment may be more important to nest survival if predators are birds, because predatory birds 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, which rely more on olfaction than 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 and hindering search efficiency by impeding movement of terrestrial predators (Martin 1992, 1993). Our results suggest that selection of a well-concealed nest site can be an effective deterrent even when there is a rich guild of predators, because concealment reduces predation risk (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 (Heusmann 1984), female body condition (Arnold et al. 1995), and nest parasitism (Brown and Brown 1981) could also influence nest survival.

Nest survival.—Brown (1981) reported a high nest success estimate (68.4%, Mayfield) over all four years of his study (1977–1980). Our Mayfield nest-success estimate was lower (~29.5%) but no 95% CL is available for historical data (P. W. Brown pers. comm.). Nonetheless, nest success of scoters at Redberry Lake is generally higher than that of 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 on account of their late nest initiations (Brown 1981, J. J. Traylor pers. obs.). That is important, because species with relatively high renesting propensity 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 renesting propensity, nest success is equivalent to hen success (Sargeant and Raveling 1992). Thus, renesting propensity is

an important determinant of the threshold level of nest survival that will sustain a population (Klett et al. 1988). Populations of ducks that nest early with a proclivity to renest require a lower threshold of nest survival rate than comparative species of ducks that nest later with lower renesting potential, given comparable adult survival. For populations of scoters to persist, 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 renesting rate; Brown 1981, J. J. Traylor unpubl. data).

Probability of daily nest survival was influenced by nest age. 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 also be related to vulnerability of the nest site (i.e. individual heterogeneity), nest initiation date, and behavior of the incubating female (see Klett and Johnson 1982). Nonetheless, effect of nest age may be confounded with that of temporal variation or individual heterogeneity (Klett and Johnson 1982, Dinsmore et al. 2002). We believe that temporal variation was not a problem, because we found samples of nests throughout the nesting cycle (Dinsmore et al. 2002, J. J. Traylor unpubl. data). Individual heterogeneity (i.e. nests differing inherently in survival) may explain differences in nest survival (Dinsmore et al. 2002). Our analyses suggested that failed (i.e. depredated and abandoned) nests were those with lower concealment, greater distance from edges, and greater proximity to water.

Use of MARK to model daily nest survival enabled us 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). Our 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 that Gadwall (*Anas strepera*) nests closer to habitat edges have higher success

rates (Pasitschniak-Arts et al. 1998, Clark and Shutler 1999). Our results are not directly comparable to the results of those studies, however, because nesting habitat on islands within Redberry Lake are composed of native field habitat with plant species mixed together, with no anthropogenic influences, such as agricultural activity (i.e. fragmentation). Thus, our measure of edge is fine-scale, rather than patch-level (i.e. planted dense nesting cover) as in those studies, and the only "real" edge, at the landscape level, may be the water surrounding the island(s) (see Stephens et al. 2003).

Conclusion.—For scoters nesting at Redberry Lake, late nest initiation date and a seemingly longer incubation period may be contributing to a decrease in nest survival by increasing the duration of exposure to predators. Furthermore, 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.

Although 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 effects on nest sites and incubating females. Nevertheless, we 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. Furthermore, because early laying is the time of highest nest mortality, concealed nest-sites are necessary to protect nests, because (1) the protracted egg-laying period (1 egg per 1.5 days in 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. having larger clutches) are thought to have higher nesting success (Flint and Grand 1996) and higher offspring survival (Guyn and Clark 1997) and, thus, contribute a higher proportion of recruits to the local population (Dzus and Clark 1998, Blums et al. 2002). Lastly, we encourage use of more biologically meaningful models to improve estimation of DSR, which provides a more valuable estimate

of nest survival through modeling of pertinent biological covariates (e.g. weather conditions, female condition, and habitat variables).

ACKNOWLEDGMENTS

We greatly appreciate financial and logistical support provided through the Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada; Canadian Wildlife Service (Prairie and Northern Region); P. Kingsmill of the Redberry Lake World Biosphere Reserve, and the University of Saskatchewan. We thank Jason Traylor and H. Remenda for their excellent field assistance; and D. Kellett, L. Hawrysh, J. Hawrysh, P. Fenig, and W. and O. Kachmarski for logistical assistance. C. Swoboda, University of Saskatchewan, provided information about nest chronology from 2002. Thanks to the many Ducks Unlimited Canada staff that helped with nest searching and especially M. Hill for coordinating searches. The 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 the Canadian Wildlife Service. The University of Saskatchewan provided personal support to J.J.T. through a Graduate Teaching Fellowship. B. Clark, K. Dufour, D. Johnson, D. Krementz, and M. Brittingham provided constructive comments on previous drafts of the manuscript.

LITERATURE CITED

- AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care. Pages 62–108 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in *Second International Symposium on Information Theory* (B. N. Petrov and F. Csádk, Eds.). Akadémiai Kiadó, Budapest, Hungary.
- ARNOLD, T. W. 1993. Factors affecting egg viability and incubation time in prairie dabbling ducks. *Canadian Journal of Zoology* 71:1146–1152.
- ARNOLD, T. W., M. G. ANDERSON, R. B. EMERY, M. D. SORENSON, AND C. N. DE SOBRINO. 1995. The effects of late-incubation body mass on reproductive success and survival of Canvasbacks and Redheads. *Condor* 97:953–962.
- BLUMS, P., R. G. CLARK, AND A. MEDNIS. 2002. Patterns of reproductive effort and success in birds: Path analyses of long-term data from European ducks. *Journal of Animal Ecology* 71:280–295.
- BROWN, P. W. 1977. Breeding biology of White-winged Scoter (*Melanitta fusca deglandi*). M.S. thesis, Iowa State University, Ames.
- BROWN, P. W. 1981. Reproductive ecology and productivity of White-winged Scoters. Ph.D. dissertation, University of Missouri, Columbia.
- BROWN, P. W., AND M. A. BROWN. 1981. Nesting biology of the White-winged Scoter. *Journal of Wildlife Management* 45:38–45.
- BRUA, R. B. 1999. Ruddy Duck nesting success: Do nest characteristics deter predation? *Condor* 101:867–870.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- CLARK, R. G., AND T. D. NUDDS. 1991. Habitat patch size and duck nesting success: The crucial experiments have not been performed. *Wildlife Society Bulletin* 19:534–543.
- CLARK, R. G., AND D. SHUTLER. 1999. Avian habitat selection: Pattern from process in nest-site use by ducks. *Ecology* 80:272–287.
- COLWELL, M. A. 1992. Phalarope nesting success is not influenced by vegetation concealment. *Condor* 94:767–772.
- COWARDIN, L. M., D. S. GILMER, AND C. W. SHAIFFER. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs*, no. 92.
- CRABTREE, R. L., L. S. BROOME, AND M. L. WOLFE. 1989. Effects of habitat characteristics on Gadwall nest predation and nest-site selection. *Journal of Wildlife Management* 53:129–137.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- DOBUSH, G. R. 1986. The accumulation of nutrient reserves and their contribution to reproductive success in the White-winged Scoter. M.S. thesis, University of Guelph, Ontario.
- DZUS, E. H., AND R. G. CLARK. 1998. Brood survival and recruitment of Mallards in relation to wetland density and hatching date. *Auk* 115:311–318.
- ERIKSTAD, K. E., J. O. BUSTNES, AND T. MOUM. 1993. Clutch-size determination in precocial birds: A study of the Common Eider. *Auk* 110:623–628.
- EVANS, M. S., M. T. ARTS, AND R. D. ROBARTS. 1996. Algal productivity, algal biomass, and zooplankton biomass in a phosphorus-rich, saline lake: Deviations from regression model predictions. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1048–1060.
- FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: Does choice of nest-site matter? *Condor* 96:761–768.

- FLINT, P. L., AND J. B. GRAND. 1996. Nesting success of Northern Pintails on the coastal Yukon Kuskokwim Delta, Alaska. *Condor* 98:54–60.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- GLOUTNEY, M. L., AND R. G. CLARK. 1997. Nest-site selection by Mallards and Blue-winged Teal in relation to microclimate. *Auk* 114:81–395.
- GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds. *Current Ornithology* 9: 63–104.
- GUYN, K. L., AND R. G. CLARK. 1997. Cover characteristics and success of natural and artificial duck nests. *Journal of Field Ornithology* 68: 33–41.
- GUYN, K. L., AND R. G. CLARK. 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. *Condor* 10:369–377.
- HAMMER, U. T., J. S. SHEARD, AND J. KRANABETTER. 1990. Distribution and abundance of littoral benthic fauna in Canadian prairie saline lakes. *Hydrobiologia* 197:173–192.
- HEUSMANN, H. W. 1984. The effects of weather on local Wood Duck production. *Journal of Wildlife Management* 48:573–577.
- JOHNSON, D. H., J. D. NICHOLS, AND M. D. SCHWARTZ. 1992. Population dynamics of breeding waterfowl. Pages 446–485 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- KEHOE, F. P. 1986. Adaptive significance of creching behavior in the White-winged Scoter (*Melanitta fusca deglandi*). M.S. thesis, University of Guelph, Ontario.
- KLETT, A. T., AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* 99:77–87.
- KLETT, A. T., T. L. SHAFFER, AND D. H. JOHNSON. 1988. Duck nest success in the Prairie Pothole Region. *Journal of Wildlife Management* 52: 431–440.
- KRASOWSKI, T. P., AND T. D. NUDDS. 1986. Microhabitat structure of nest sites and nesting success of diving ducks. *Journal of Wildlife Management* 50:203–208.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- LINDEMAN, D. H., AND R. G. CLARK. 1999. Relationships between the distribution of Lesser Scaup (*Aythya affinis*) and amphipods in Saskatchewan wetlands. *Wetlands* 19:627–638.
- LIVEZEY, B. C. 1981. Location and success of duck nests evaluated through discriminant analysis. *Wildfowl* 32:23–27.
- LOKEMOEN, J. T., AND R. O. WOODWARD. 1992. Nesting waterfowl and water birds on natural islands in the Dakotas and Montana. *Wildlife Society Bulletin* 20:163–171.
- MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 in *Ecology and Conservation of Neotropical Migrant Landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- MARTIN, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. *BioScience* 43:523–532.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MENDENHALL, V. M., AND H. MILNE. 1985. Factors affecting duckling survival of eiders (*Somateria mollissima*) in Northeast Scotland. *Ibis* 127: 148–158.
- OLSON, R., AND F. C. ROHWER. 1998. Effects of human disturbance on success of artificial duck nests. *Journal of Wildlife Management* 62:1142–1146.
- OWEN, M., AND J. M. BLACK. 1990. *Waterfowl Ecology*. Chapman and Hall, New York.
- PASITSCHNIK-ARTS, M., R. G. CLARK, AND F. MESSIER. 1998. Duck nesting success in a fragmented prairie landscape: Is edge effect important? *Biological Conservation* 85:52–62.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- ROTELLA, J. J., M. L. TAPER, AND A. J. HANSEN. 2000. Correcting nesting-success estimates for observer effects: Maximum-likelihood estimates of daily survival rates with reduced bias. *Auk* 117:92–109.
- SARGEANT, A. B., AND D. G. RAVELING. 1992. Mortality during the breeding season. Pages 396–422 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- SAS INSTITUTE. 1989. *SAS Language and Procedures: Usage*, 1st ed., version 6. SAS Institute, Cary, North Carolina.
- SCHIECK, J. O., AND S. J. HANNON. 1993. Clutch predation, cover and the overdispersion of nests of the Willow Ptarmigan. *Ecology* 74:743–750.
- STEPHENS, S. S., D. N. KOONS, J. J. ROTELLA, AND D. W. WILLEY. 2003. Effects of habitat fragmentation on avian nesting success: A review of the evidence at multiple spatial scales. *Biological Conservation* 111:101–110.

- STOKES, D. L., AND P. D. BOERSMA. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*). *Auk* 115:34–49.
- TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. *American Midland Naturalist* 111:1–7.
- TOMBRE, I. M., AND K. E. ERIKSTAD. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. *Journal of Animal Ecology* 65: 325–331.
- TRAYLOR, J. J. 2003. Nesting and duckling ecology of White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan. M.S. thesis, University of Saskatchewan, Saskatoon.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* 63:281–288.
- WELLER, M. V. 1956. A simple candler for waterfowl eggs. *Journal of Wildlife Management* 20: 1111–1113.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120–139.
- Associate Editor: M. Brittingham