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EFFECTS OF INTRINSIC AND EXTRINSIC FACTORS ON SURVIVAL OF WHITE-WINGED SCOTER (*MELANITTA FUSCA DEGLANDI*) DUCKLINGS

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ABSTRACT.—In waterfowl, offspring survival and the effects of extrinsic (i.e. weather, hatching date) and intrinsic (i.e. physical and nutritional traits of individual females and ducklings, brood sizes) factors on it are poorly understood. In 2000 and 2001, we estimated duckling and brood survival of White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan, Canada, to 30 days of age to examine 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, (5) maternal female size and body condition at hatch, and (6) weather. We estimated survival with Cormack-Jolly-Seber models, in program MARK, from observations of individually marked adult females ($n = 94$) and ducklings ($n = 664$). Most mortality (i.e. 0.80 and 0.95 for each year, respectively) occurred within six days of hatch in both years. Duckling survival probability decreased with advancing hatch date; increased with larger initial brood sizes; was higher for larger, better-conditioned ducklings; and increased with favorable weather. Brood survival decreased with advancing hatch date, increased with larger initial brood sizes, and increased with favorable weather. For 2000 and 2001, our models predict survival probabilities of ducklings (0.0061 and 0.0027, respectively) and broods (0.015 and 0.00048, respectively) that are lower than any previously reported. We suspect that intense gull (*Larus* spp.) predation shortly after hatch had the largest influence on duckling survival, though results also underscore the significance of intrinsic factors. Received 16 September 2004, accepted 11 May 2005.

Key words: brood size, duckling body size, extrinsic factors, hatching date, program MARK, survival estimation.

Effets des Facteurs Intrinsèques et Extrinsèques sur la Survie les Jeunes de *Melanitta fusca deglandi*

RÉSUMÉ.—Chez la sauvagine, la survie de la progéniture et les effets des facteurs extrinsèques (i.e. conditions climatiques, date d'éclosion) et intrinsèques (i.e. traits physiques et nutritionnels des femelles et des jeunes, taille de couvée) sur cette même survie sont encore mal compris. En 2000 et 2001, nous avons estimé la survie des jeunes et des couvées de *Melanitta fusca deglandi* à Redberry Lake, Saskatchewan, Canada, jusqu'à l'âge de 30 jours afin d'examiner les relations entre la survie des jeunes et (1) la date d'éclosion, (2) la taille de couvée initiale à l'éclosion, (3) la taille et la condition physique des jeunes à l'éclosion, (4) le sexe de la progéniture, (5) la taille de la mère et sa condition physique lors de l'éclosion, et (6) les conditions climatiques.

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Nous avons estimé la survie avec des modèles de Cormack-Jolly-Seber, dans le programme MARK, à partir d'observations de femelles adultes individuellement marquées ($n = 94$) et de jeunes ($n = 664$). La plupart des mortalités (i.e. 0,80 et 0,95 pour chaque année, respectivement) ont eu lieu dans une période de 6 jours après éclosion pour les deux années. La probabilité de survie des jeunes a diminué avec des dates d'éclosions précoces, elle a augmenté avec des tailles de couvées initiales plus grosses, elle était meilleure pour les jeunes de plus grande taille et en meilleurs conditions, et elle augmentait avec des conditions climatiques favorables. La survie des couvées a diminué avec des dates avancées d'éclosion, augmentait avec une taille de couvée initiale plus grosse, et augmentait avec des conditions climatiques favorables. Pour 2000 et 2001, nos modèles prédisent des probabilités de survie plus faibles, que ce qui a été précédemment rapporté, chez les jeunes (0,0061 et 0,0027, respectivement) et les couvées (0,015 et 0,00048, respectivement). Nous suspectons que la prédation intense par les mouettes et les goélands (*Larus* spp.) peu de temps après l'éclosion a eu la plus grande influence sur la survie des jeunes, bien que les résultats sous-estiment également la signification des facteurs intrinsèques.

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). Recent 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 have enabled researchers to draw inferences about the interplay of ecological covariates and offspring survival. However, few studies have estimated the effect size of extrinsic (i.e. unpredictable inclement weather and hatching date) and intrinsic (i.e. physical and nutritional traits of individual females and ducklings, and brood sizes) factors frequently hypothesized to influence survival probabilities in ducklings (Guyn and Clark 1999, Gendron and Clark 2002). Here, we use individually marked adult females and ducklings to investigate duckling and brood survival in relation to such factors.

Duckling survival typically is lowest during the first 10 days after hatch in waterfowl and usually stabilizes by 30 days (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 and their offspring. For example, ducklings that hatch early can have higher survival rates (Krapu et al. 2000, Pelayo and Clark 2003), though this finding is not ubiquitous (Dawson and Clark 1996, Gendron and Clark 2002). 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 can be variable (Guyn and Clark 1999, Gendron and Clark 2002). In addition, female traits such as structural size and body condition may influence duckling survival. For instance, Gendron and Clark (2002) found that Gadwall (*Anas strepera*) ducklings had higher survival probabilities if accompanied by larger females in better nutritional condition, though some studies failed to demonstrate a connection (Arnold et al. 1995, Blums et al. 2002).

Duckling traits, including size, body condition, and sex, may also be important determinants of duckling survival. Larger ducklings can have higher survival probabilities than smaller ducklings (Christensen 1999, Pelayo and Clark 2003). However, sex differences in offspring survival have received little attention, and studies of duckling survival in relation to their sex have had contrasting results (Dawson and Clark 1996, Korschgen et al. 1996). Studies of the influence of weather on offspring survival also are scarce, though adverse weather conditions (i.e. rain, cold, or wind) can decrease duckling survival probabilities, as predicted (Korschgen et al. 1996; see Johnson et al. 1992).

White-winged Scoters (*Melanitta fusca deglandi*; hereafter "scoters") on Redberry Lake, Saskatchewan, Canada, are ideal subjects for testing hypotheses about sources of variation in duckling survival for several reasons: (1)

large numbers of nests are readily accessible on islands of Redberry Lake, so ducklings can be marked *en masse*; (2) broods are highly visible, because emergent aquatic vegetation is absent; (3) broods are subject to avian predation; and (4) ducklings complete their growth on the lake (Brown and Fredrickson 1989, Kehoe 1989). Our main objective was to estimate duckling survival in relation to intrinsic and extrinsic variables. We 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, (5) maternal female size and body condition at hatch, and (6) weather. Total brood loss often accounts for most offspring mortality (Talent et al. 1983, Mauser et al. 1994); thus, we considered survival probability from the standpoint of individual ducklings as well as of entire broods.

METHODS

Study area.—We conducted field work at Redberry Lake, a 4,500-ha migratory bird sanctuary in Saskatchewan, Canada (52°43'N, 107°09'W), from June to October, 2000–2001 (Fig. 1). Redberry Lake is within the aspen parkland biome, surrounded by rolling hills, numerous small wetlands, and small-grain agriculture (Brown and Fredrickson 1989). Water levels have dropped 10 m since 1940, and the lake is presently mesosaline (i.e. 20–50 g L⁻¹; total dissolved solids 20.9 g L⁻¹) (Waiser and Robarts 1995). Lake water was characterized by depths of 1–3 m along shorelines and an average depth of 9.3 m. California (*Larus californicus*) and Ring-billed (*L. delawarensis*) gulls nested on New Tern and Pelican Island within the lake. Additional description of the study area is given in Traylor et al. (2004a).

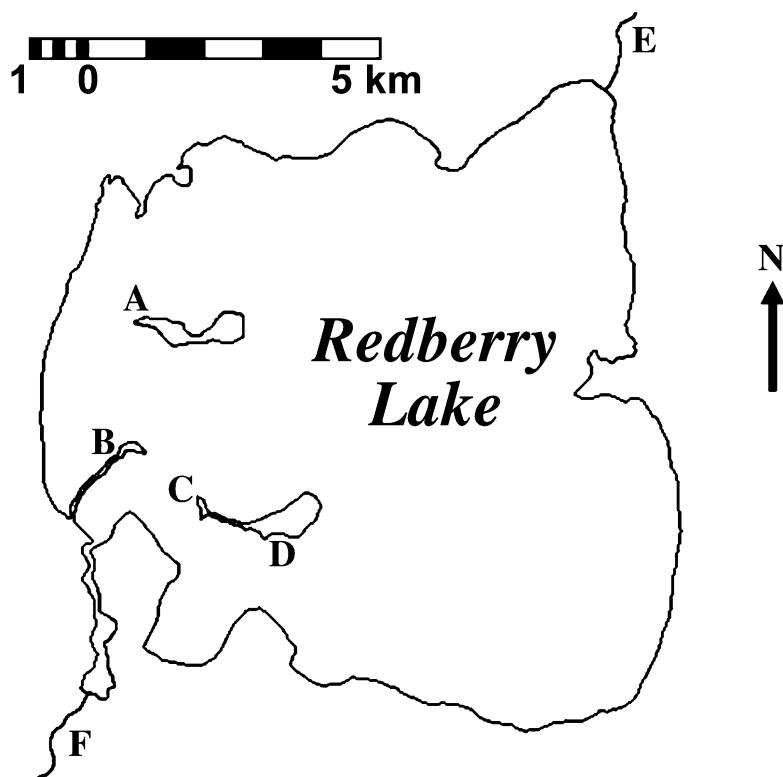


FIG. 1. Redberry Lake federal bird sanctuary and Biosphere Reserve, Saskatchewan, Canada. Letters within and around the lake indicate (A) Gull Island, (B) Old Tern Peninsula, (C) New Tern Island, (D) Pelican Island, (E) Oscar Creek, and (F) Marshy Creek.

Capture and marking.—Nest searches were done as described in Traylor et al. (2004a). After final clutch size was attained, eggs were uniquely labeled with indelible ink, and length (L) and width (W) were measured (to the nearest 0.1 mm with dial calipers). Egg size was obtained with Hoyt's (1979) equation: volume (cm^3) = $0.000507LW^2$.

Nests were visited near the end of the 28-day incubation period, just before or during hatch, as predicted by aging nests by candling eggs (Weller 1956); duckling bills protruding from 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 by hand on the nest or with a hand-held net as they flushed from the nest. Females were weighed with a Pesola scale (to the nearest 10 g), measured (culmen, head length, and tarsal length were taken with dial calipers to the nearest 0.1 mm), and given a standard federal leg band and a uniquely colored nasal-marker (Lokemoen and Sharp 1985). Hatched ducklings were captured on nests, weighed (to the nearest 0.5 g), measured (culmen, head, and tarsus length to the nearest 0.01 mm), sexed by cloacal examination (in 2001 only), marked with a plasticine leg band (Blums et al. 1999), and given a uniquely colored nape-marker for individual identification (Pelayo and Clark 2003, J. T. Pelayo et al. unpubl. data). Ducklings were then returned to nests from which they were initially removed and covered with nesting material. Initial brood size was calculated by subtracting the number of eggs that did not hatch from the final clutch size and the ducklings left behind or dead in the nest.

Observation of marked females and ducklings.—We obtained weather data from a weather station at Redberry Lake that included daily maximum, minimum, and mean temperature ($^{\circ}\text{C}$); humidity (%; i.e. amount of water vapor in air at a given temperature); rainfall (mm); and wind speed (km h^{-1}). To estimate duckling survival after hatch, we observed nasal-marked females and nape-marked ducklings on all days with no rain and moderate wind ($\leq 25 \text{ km h}^{-1}$). We read marks using 15–56 \times binoculars or 30–80 \times spotting scope from a boat or shoreline when ducklings were most active (0700–1200 and 1600–2100 hours). Because emergent vegetation was absent, we had clear visibility, which

ensured accurate identification of ducklings from marks (Brown and Fredrickson 1989). We monitored duckling survival only until they were 30 days old, because survival rates are often constant thereafter (Grand and Flint 1996, Guyn and Clark 1999). Use of individually marked ducklings and females enabled us to account for total brood mortality.

Statistical analysis.—We used an analysis of covariance (ANCOVA) to test whether brood size varied annually and with hatch date (PROC GLM; SAS Institute 1990). To correct for hatch date effects, we standardized brood size for hatch date by using residuals from this analysis in all subsequent analyses. We then tested for annual differences in hatch dates using general linear models (PROC GLM; SAS Institute 1990).

Principal component analysis (PCA; PROC PRINCOMP; SAS Institute 1990) was used to derive multivariate indices of body size separately for adult females and ducklings, on the basis of the correlation matrix of tarsus, culmen, and head lengths (Freeman and Jackson 1990). We used residuals from a general linear model (PROC GLM; SAS Institute 1990) to acquire indices of adult female body condition (i.e. size-adjusted body mass) adjusted with incubation stage, nest initiation date, and structural size (Alisauskas and Ankney 1990). Duckling body weight was also regressed (PROC GLM; SAS Institute 1990) on structural size, and hatch date and residuals were used as an index of body condition. All linear trends were confirmed by visual inspection of data plots.

A univariate weather index was generated for each duckling for the first seven days after hatch in 2001 only. A PCA of the correlation matrix resulted in a first principal component (PC1) with loadings of -0.50 , 0.64 , and 0.58 for mean temperature ($^{\circ}\text{C}$), mean humidity (%), and mean maximum wind speed (km h^{-1}), respectively. Mean humidity was used rather than mean precipitation because there were numerous days with trace rainfall amounts. The first principal component accounted for 69% of the summed variance of the three input variables. Hence, PC1 scores corresponded to days that were colder, more humid, and windier than days with negative values.

Duckling survival.—Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) in MARK (White and Burnham 1999) were used to compute maximum-likelihood estimates of probabilities

for apparent survival (ϕ_i) and resighting probability (p_i) of marked ducklings during the first 30 days of age. Ducklings do not leave the lake before fledging (~8 weeks of age), so we 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 (days) survives until age $i + 1$ and does not permanently emigrate. We defined resighting probability (p_i) as the probability that a marked individual alive at age i is seen. Initial encounter histories were 32 occasions (t_0 to t_{31}), but initial convergence problems during estimation forced us to pool daily resightings into 15 two-day intervals (2-day products of daily survival) corresponding to 16 encounter occasions. Consequently, we defined duckling survival as the probability of surviving to 30 days of age, whereas brood survival was defined as the probability of at least one duckling per brood surviving to 30 days of age. We used the logit-link function to constrain all estimates of parameters to the interval (0 to 1; Lebreton et al. 1992).

We developed a set of models based on biological hypotheses about offspring survival to 30 days (Burnham and Anderson 2002). We first considered a global model that included parameters hypothesized to vary with year and duckling age (a, days) $\{S_{\text{year} \times a} p_{\text{year} \times a}\}$ (i.e. interactions between year and age). We then used goodness-of-fit testing (GOF) to determine whether our global model met assumptions of homogeneity and independence. For duckling- and brood-level analyses, GOF tests for the global model were done with a parametric bootstrap method in MARK (White and Burnham 1999). The variance inflation factor (\hat{c}) was adjusted to account for lack of model fit (see Burnham and Anderson 2002). We calculated \hat{c} by dividing the deviance of the global model by the mean deviance from 500 bootstrap iterations, resulting in $\hat{c} = 1.27$ for the duckling-level analysis and $\hat{c} = 1.17$ for the brood-level analysis.

After we considered a global model, reduced parameter models were constructed assessing year- and age-specificity between S_i and p_i ; all combinations of year and age dependency and independency were tested. We also fitted parameters to linear (A) and quadratic trends ($A + A^2$) with age, by manipulating design matrices in MARK to check for nonlinearity of trends with age. We considered slopes of relationships

between age and year to be different (*, interactive) and parallel (+, additive). We estimated slopes between survival and individual-level covariates of interest by manipulating design matrices. Covariates were added to the most parsimonious model to consider additional structure; subsequently, we estimated 95% confidence limits (CL) of slopes between two-day survival probabilities and n^{th} covariates of interest, denoted 95% CL ($\hat{\beta}_n$). Covariates were hatch date (hd), quadratic effect of hatch date ($\text{hd} + \text{hd}^2$), brood size (bs), female condition (fc), female size (fs), duckling size (ds), and duckling condition (dc). We considered quadratic effect of hatch date on survival to examine whether there was a greater cost of hatching very early or late compared with the approximate median date (~15 days). We also considered *a priori* two-way interactions (i.e. hatch date * duckling size, hatch date * duckling condition) specifically to be of ecological interest; otherwise, models were constrained to be additive over potential combinations of covariates. In addition, for 2001 data only, we used duckling sex (s) and PC1 scores of weather (w) as covariates to improve model fit. Size, condition, and sex of individual ducklings could not be included in brood-level analyses. We considered models where covariates were entered singularly and combined with other covariates. Relationships between year and covariates were considered to be interactive or additive in models containing single covariates or all possible covariates. All covariates were standardized as $(x_i - \bar{x})/\text{SD}$ in MARK.

The most parsimonious model was selected on the basis of the quasi-likelihood Akaike's Information Criterion (QAIC_c) to correct for small sample size and lack of fit from overdispersion (Burnham and Anderson 2002). We used model weight (w_i) to evaluate likelihood of each model; w_i are normalized Akaike weights and indicate the relative support for different models in the candidate model set and can be interpreted as evidence that a model is the most plausible, given the data and model set (Burnham and Anderson 2002). We summed w_i of all models (i.e. Σw_i) with a given covariate and used this as a metric assessing importance to survival (Burnham and Anderson 2002). To accommodate model uncertainty, we generated model-averaged parameters (i.e. survival, resighting, and $\hat{\beta}_1$ of covariates) and unconditional standard errors from all models in the

candidate set after weighting by appropriate w_i using MARK (Burnham and Anderson 2002). Associated variances for 30-day survival probabilities were calculated using the Delta method to account for covariance between estimates across survival periods (Williams et al. 2002). Back transformation of slopes and intercepts was required to make predictions about $S|x_1 \dots x_n$ following

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

Asymptotic 95% CL were also calculated by back-transforming from logit values estimated from the upper and lower 95% CL of covariates. Unless otherwise indicated, tests were two-tailed, with significance levels set at $P < 0.05$.

RESULTS

Marked individuals and brood size.—For 2000 and 2001, we observed 35 and 59 nasal-marked females and 265 and 399 ducklings individually marked with nape-markers, respectively. That resulted in 507 and 588 sightings of marked ducklings and 127 and 144 sightings of broods containing marked ducklings or females 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) ($F = 0.14$, $df = 1$ and 107, $P = 0.75$). Range of initial brood sizes was 1–13 ducklings, with similar average initial brood sizes in 2000 ($\bar{x} = 7.6$, 95% CL: 6.8 to 8.4, $n = 35$) and 2001 ($\bar{x} = 6.8$, 95% CL: 6.3 to 7.4, $n = 59$) ($F = 1.44$, $df = 2$ and 91, $P = 0.23$), though brood size declined with later hatch dates ($F = 15.49$, $df = 1$ and 92, $r^2 = 0.14$, $P = 0.0002$; slope = -0.19 , 95% CL: -0.10 to -0.28).

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 of adult females. Adult female body mass was positively correlated with PC1 ($F = 16.22$, $df = 1$ and 93, $r^2 = 0.14$, $P < 0.0001$); therefore, residuals from regression analysis were used as an index of female body condition. Mean female mass at hatch was 1,102 g (95% CL: 1,089 to 1,115 g), with a range of 950–1,240 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 of ducklings. Residuals from regression were used as a body condition index for each duckling because body mass was positively correlated with PC1 ($F = 102.35$, $df = 1$ and 662, $r^2 = 0.13$, $P < 0.0001$). The range of duckling mass at hatch was 39.0–63.0 g ($\bar{x} = 52.5$ g, 95% CL: 52.2 to 52.8 g). Eggs were measured for 490 of 664 marked ducklings. Mean egg volume was 72.7 cm³ (95% CL: 72.3 to 73.1 cm³), with a range of 57.2–83.6 cm³. Larger eggs produced structurally larger ($F = 105.57$, $df = 1$ and 488, $r^2 = 0.18$, $P \leq 0.0001$; slope = 1.43, 95% CL: 1.15 to 1.70), heavier ($F = 744.84$, $df = 1$ and 488, $r^2 = 0.60$, $P \leq 0.0001$; slope = 0.86, 95% CL: 0.80 to 0.92), and better-conditioned ducklings ($F = 377.73$, $df = 1$ and 488, $r^2 = 0.44$, $P \leq 0.0001$; slope = 0.79, 95% CL: 0.71 to 0.87). Duckling sex was determined only in 2001; there were 196 male and 203 female ducklings, respectively (49:51 sex ratio). Male ducklings were structurally larger ($F = 29.46$, $df = 1$ and 397, $P \leq 0.0001$), in slightly poorer condition ($F = 3.92$, $df = 1$ and 397, $P = 0.048$), but had similar body masses ($F = 0.08$, $df = 1$ and 397, $P = 0.77$) as compared with female ducklings; there was no difference in egg size between sexes ($F = 1.89$, $df = 1$ and 271, $P = 0.17$).

Survival and resighting probabilities of ducklings and broods.—In 2000, duckling survival was 0.0061 (95% CL: -0.0027 to 0.015); whereas in 2001, it was 0.0027 (95% CL: -0.0020 to 0.0073). Brood survival was 0.015 (95% CL: -0.017 to 0.046) in 2000 and 0.00048 (95% CL: -0.00079 to 0.0017) in 2001. Bidaily survival probability of ducklings for the first 18 days of age was slightly lower in 2001 than in 2000 (Fig. 2), but was higher from day 22 to 30 of age in 2001 (Fig. 2). Duckling mortality was greatest during the first two days of age in both years, estimated as 0.53 and 0.68 of all losses during 2000 and 2001, respectively (Fig. 3). Furthermore, 0.80 and 0.95 of duckling losses occurred within six days of age in 2000 and 2001, respectively (Fig. 3). Resighting probability was similar between years but differed markedly from ages 14 to 19. Mean resighting probabilities of ducklings were 0.36 (95% CL: 0.22 to 0.50) in 2000 and 0.46 (95% CL: 0.26 to 0.66) in 2001, whereas for broods they were 0.40 (95% CL: 0.19 to 0.61)

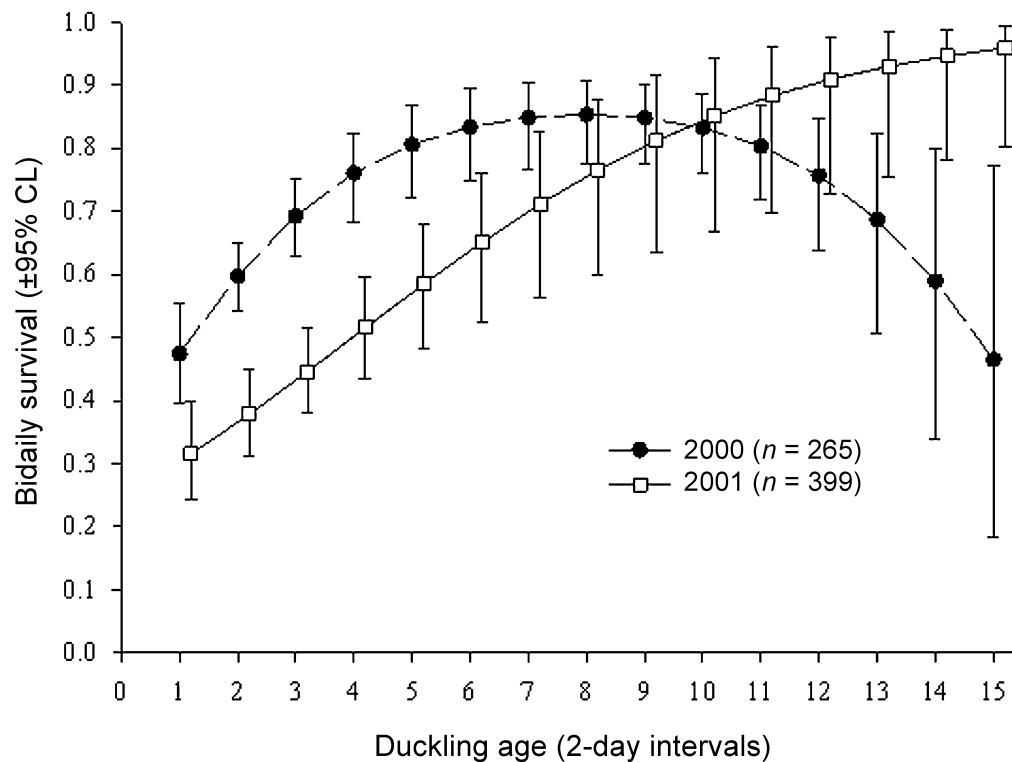


FIG. 2. 95% CL of model-averaged estimates for 2-day (bidaily) survival rates of White-winged Scoter ducklings to 30 days of age. Data were collected at Redberry Lake, Saskatchewan, Canada, in 2000 ($n = 265$) and 2001 ($n = 399$).

and 0.50 (95% CL: 0.40 to 0.60) in 2000 and 2001, respectively.

Correlates of duckling and brood survival.—Model selection based on QAIC_c suggested that duckling survival was a quadratic function of age ($\hat{\beta}_A = 0.58$, 95% CL: 0.23 to 0.93; $\hat{\beta}_{A^2} = -0.03$, 95% CL: -0.07 to -0.01) in 2000, but a linear trend with age ($\hat{\beta}_A = 0.28$, 95% CL: 0.14 to 0.42) in 2001. The best approximating model {1} ($w_i = 0.331$, $\Delta\text{QAIC}_c = 0.00$) included additive effects of hatching date, brood size, duckling condition, duckling size, weather, and an interaction between hatch date and duckling condition (Table 1). Support was also obtained for model {2} ($w_i = 0.202$, $\Delta\text{QAIC}_c = 0.99$), which included female condition as an influence on duckling survival (Table 1). Model {3} ($w_i = 0.167$, $\Delta\text{QAIC}_c = 1.37$) also received some support, which, unlike higher-ranked models, contained effects of female size; all other models had $\Delta\text{QAIC}_c \geq 3.90$ (Table 1).

There was strong evidence that duckling survival declined with hatching date ($\hat{\beta}_{hd} = -0.36$, 95% CL: -0.55 to -0.16; $\Sigma w_i = 0.997$), increased with initial brood size ($\hat{\beta}_{bs} = 0.42$, 95% CL: 0.26 to 0.58; $\Sigma w_i = 0.999$) (Fig. 4A), increased with duckling condition ($\hat{\beta}_{dc} = 0.20$, 95% CL: 0.05 to 0.35; $\Sigma w_i = 0.938$), increased with duckling size ($\hat{\beta}_{ds} = 0.27$, 95% CL: 0.12 to 0.43; $\Sigma w_i = 0.997$), and decreased with adverse weather ($\hat{\beta}_w = -0.72$, 95% CL: -0.93 to -0.50; $\Sigma w_i = 0.999$) (Fig. 4B). There was also an interaction between hatch date and duckling condition ($\hat{\beta}_{hd*dc} = -0.22$, 95% CL: -0.39 to -0.04; $\Sigma w_i = 0.784$); thus, survival probability of ducklings in good condition was higher compared with ducklings in poorer condition; this disparity increased as hatch dates progressed.

There was moderate evidence that duckling survival decreased with female condition ($\hat{\beta}_{fc} = -0.07$, 95% CL: -0.21 to 0.07; $\Sigma w_i = 0.285$) and increased with female size ($\hat{\beta}_{fs} = 0.08$, 95%

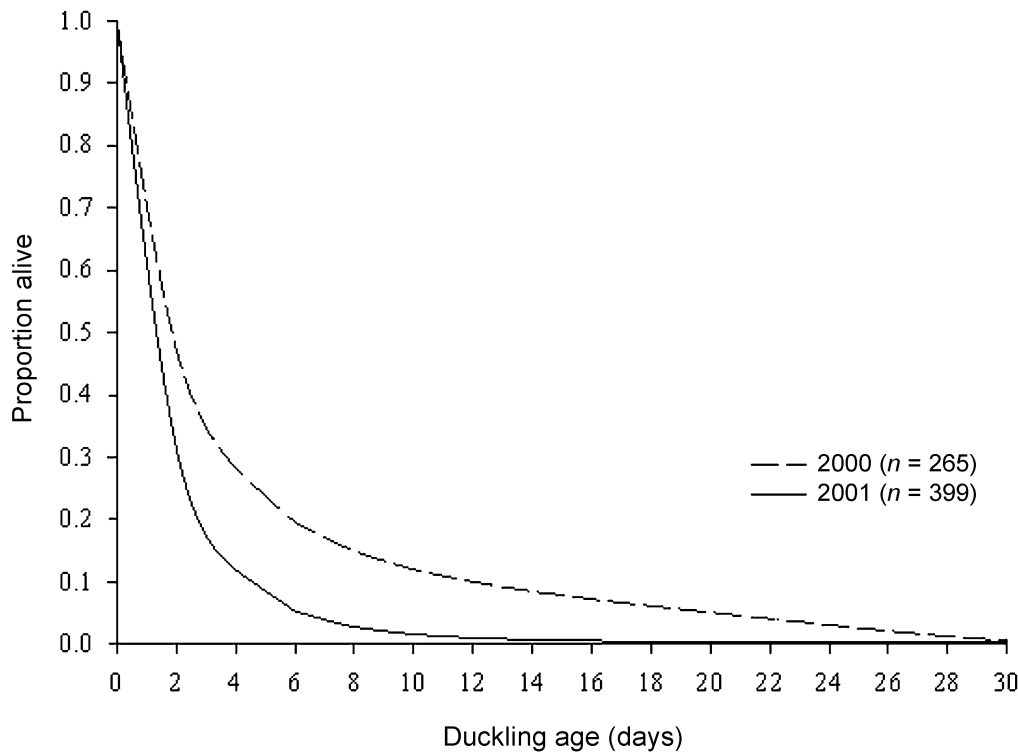


FIG. 3. Proportion of White-winged Scoter ducklings surviving by age at Redberry Lake, Saskatchewan, Canada, for 2000 ($n = 265$) and 2001 ($n = 399$).

TABLE 1. Summary of model selection for estimation of survival (S) and resighting probability (p) of White-winged Scoter ducklings on Redberry Lake, Saskatchewan, Canada, for 2000 and 2001. Only models with $\Delta\text{QAIC}_c < 6$ are considered here, ranked by ascending ΔQAIC_c .

Number and model ^a	QAIC _c ^b	ΔQAIC_c ^c	w_i ^d	K ^e	Q_{deviance} ^f
1 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{dc}+\text{ds}+\text{hd}^*\text{dc}+\text{w}} p_{\text{year}^*a}\}$	1706.75	0.00	0.331	38	1628.02
2 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{fc}+\text{dc}+\text{ds}+\text{hd}^*\text{dc}+\text{w}} p_{\text{year}^*a}\}$	1707.74	0.99	0.202	39	1626.86
3 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{fs}+\text{dc}+\text{ds}+\text{hd}^*\text{dc}+\text{w}} p_{\text{year}^*a}\}$	1708.12	1.37	0.167	39	1627.41
4 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{dc}+\text{ds}+\text{w}} p_{\text{year}^*a}\}$	1710.65	3.90	0.047	37	1634.06
5 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{dc}+\text{ds}+\text{fs}+\text{w}} p_{\text{year}^*a}\}$	1711.54	4.79	0.030	38	1632.81
6 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{ds}+\text{hd}^*\text{dc}+\text{w}} p_{\text{year}^*a}\}$	1712.02	5.27	0.024	37	1635.43
7 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{dc}+\text{ds}+\text{fc}+\text{w}} p_{\text{year}^*a}\}$	1712.27	5.52	0.021	38	1633.54
8 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{hd}2+\text{bs}+\text{dc}+\text{ds}+\text{w}} p_{\text{year}^*a}\}$	1712.41	5.65	0.020	38	1633.68
9 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{fs}+\text{ds}+\text{hd}^*\text{dc}+\text{w}} p_{\text{year}^*a}\}$	1712.63	5.88	0.017	38	1633.90
10 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{dc}+\text{ds}+\text{fc}+\text{fs}+\text{w}} p_{\text{year}^*a}\}$	1712.75	6.00	0.016	39	1631.88
11 $\{S_{\text{year}^*A+A^200+\text{hd}+\text{bs}+\text{dc}+\text{ds}+\text{s}+\text{w}} p_{\text{year}^*a}\}$	1712.75	6.00	0.016	38	1634.03

^a Models are denoted as additive models (+) or models with interaction (*); factors included year effects (00 = 2000, 01 = 2001, and year), duckling age dependency (a), linear trend with age (A), quadratic trend with age ($A+A^2$), 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 (hd^*dc), hatch date * duckling size (hd^*ds), duckling sex (s), and weather (w, in 2001 only).

^b Quasi-likelihood Akaike's Information Criterion with small sample correction.

^c Difference in QAIC_c values between the model with the lowest QAIC_c value.

^d Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).

^e Number of estimable parameters.

^f Q_{deviance} is difference between $-2\log$ -likelihood of the current model and that of the saturated model.

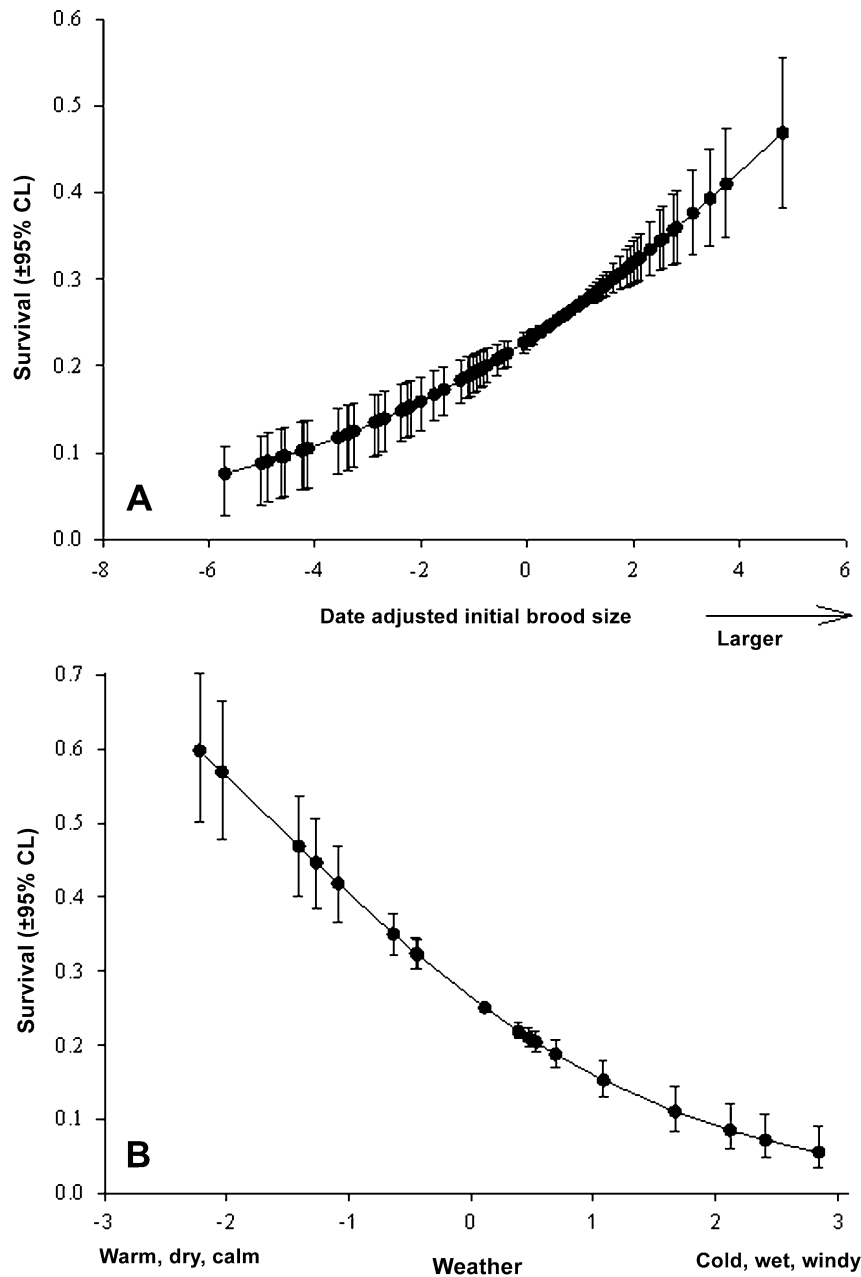


FIG. 4. Relationships between White-winged Scoter duckling survival and (A) initial brood size at hatch ($\beta_{bs} = 0.42$, 95% CL = 0.26 to 0.58, $n = 94$) combined for 2000 and 2001, and (B) weather during the first week after hatch ($\beta_w = -0.72$, 95% CL = -0.93 to -0.50 , $n = 399$) in 2001 only at Redberry Lake, Saskatchewan, Canada. Survival estimates are model averages back-transformed from a logit scale. Index of initial brood size used date-corrected residuals, and the weather index was calculated using principal component analysis.

CL: -0.08 to 0.24 ; $\Sigma w_i = 0.271$). There was no relationship between female condition and hatch date or initial brood size (all $P \geq 0.40$), which suggests that females in better condition at hatch did not nest earlier or have larger brood sizes at hatch. There was no support for a quadratic effect of hatch date ($\hat{\beta}_{hd} = -0.32$, 95% CL: -0.51 to -0.14 ; $\hat{\beta}_{hd^2} = 0.06$, 95% CL: -0.09 to 0.22 ; $\Sigma w_i = 0.06$), duckling sex ($\hat{\beta}_s = 0.02$, 95% CL: -0.18 to 0.23 ; $\Sigma w_i = 0.046$), or an interaction between hatch date and duckling size ($\hat{\beta}_{hd*ds} = -0.01$, 95% CL: -0.17 to 0.15 ; $\Sigma w_i = 0.034$) on survival. Resighting probability was modeled best with stochastic age dependency among years (i.e. year * age).

Among the candidate set of brood-level models, the best model {1} ($w_i = 0.330$, $\Delta QAIC_c = 0.00$) was structured, such that brood survival exhibited parallel quadratic trends with age in 2000 and 2001 ($\hat{\beta}_A = 0.56$, 95% CL: 0.19 to 0.94 ; $\hat{\beta}_{A^2} = -0.03$, 95% CL: -0.06 to -0.01) (Table 2). Brood survival showed additive relationships with hatching date, brood size, and weather. Support was also obtained for model {2} ($w_i = 0.174$, $\Delta QAIC_c = 1.28$), which allowed for the inclusion of a quadratic effect of hatch date on brood survival. There was also some support for model {3} ($w_i = 0.155$, $\Delta QAIC_c = 1.51$), which was different from the other top models in the incorporation of female size; all other models had $\Delta QAIC_c \geq 2.26$ (Table 2).

There was strong evidence that brood survival decreased with hatch date ($\hat{\beta}_{hd} = -0.78$, 95% CL: -1.25 to -0.32 ; $\Sigma w_i = 0.993$), increased with initial brood size ($\hat{\beta}_{bs} = 0.90$, 95% CL: 0.50 to 1.29 ; $\Sigma w_i = 0.999$), and decreased with inclement weather ($\hat{\beta}_w = -0.80$, 95% CL: -1.23 to -0.37 ; $\Sigma w_i = 0.996$). There was moderate evidence that brood survival increased and then decreased (i.e. quadratic effect) with advancing hatch date ($\hat{\beta}_{hd} = -0.79$, 95% CL: -1.23 to -0.33 ; $\hat{\beta}_{hd^2} = -0.19$, 95% CL: -0.52 to 0.15 ; $\Sigma w_i = 0.350$), decreased with female condition ($\hat{\beta}_{fc} = -0.05$, 95% CL: -0.37 to 0.27 ; $\Sigma w_i = 0.243$), and increased with female size ($\hat{\beta}_{fs} = 0.15$, 95% CL: -0.15 to 0.46 ; $\Sigma w_i = 0.330$). Resighting probability of broods varied stochastically with age (age dependent) in 2000, but was constant in 2001 (i.e. p_{00a01}).

DISCUSSION

Duckling and brood survival.—Our estimates of duckling and brood survival are the lowest published for ducks, to our knowledge (see Grand and Flint 1996, Guyn and Clark 1999, Gendron and Clark 2002), unbiased by any failure to account for detection probability. Moreover, all known studies of scoters (Hildén 1964, Brown and Frederickson 1989, Mikola et al. 1994, present study) suggest consistently low survival of ducklings; even in years of highest survival,

TABLE 2. Model selection for estimation of survival (S) and resighting probability (p) of White-winged Scoter broods on Redberry Lake, Saskatchewan, Canada, for 2000 and 2001. Only those models with $\Delta QAIC_c < 6$ are considered here, ranked by ascending $\Delta QAIC_c$.

Number and model ^a	QAIC _c ^b	$\Delta QAIC_c$ ^c	w_i ^d	K ^e	Q _{deviance} ^f
1 {S _{year+A+A²+hd+bs+w} p _{00a01} }	618.91	0.00	0.330	21	573.17
2 {S _{year+A+A²+hd+hd²+bs+w} p _{00a01} }	620.19	1.28	0.174	22	572.08
3 {S _{year+A+A²+hd+bs+fs+w} p _{00a01} }	620.42	1.51	0.155	22	572.31
4 {S _{year+A+A²+hd+bs+fc+w} p _{00a01} }	621.17	2.26	0.107	22	573.05
5 {S _{year+A+A²+hd+hd²+bs+fs+w} p _{00a01} }	621.52	2.61	0.089	23	571.01
6 {S _{year+A+A²+hd+bs+fc+fs+w} p _{00a01} }	622.56	3.65	0.053	23	572.06
7 {S _{year+A+A²+hd+hd²+bs+fc+w} p _{00a01} }	622.57	3.66	0.053	23	572.07
8 {S _{year+A+A²+hd+hd²+bs+fc+fs+w} p _{00a01} }	623.86	4.95	0.027	24	570.94

^a Models are denoted as additive models (+); factors included year effects (00 = 2000, 01 = 2001, and year), brood-age dependency (a), linear trend with age (A), quadratic trend with age (A+A²), constant daily resighting (.), hatch date (hd), quadratic hatch date (hd + hd²), initial brood size (bs), female condition (fc), female size (fs), and weather (w, in 2001 only).

^b Quasi-likelihood Akaike's Information Criterion with small sample correction.

^c Difference in QAIC_c values between the model with the lowest QAIC_c value.

^d Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 2002).

^e Number of estimable parameters.

^f Q_{deviance} is difference between -2 log-likelihood of the current model and that of the saturated model.

0.90 to 0.95 of all ducklings died. In accord with the findings of Alisauskas et al. (2004) that suggest no *in situ* recruitment of ducklings into the Redberry Lake breeding population of scoters, our estimates suggest very low potential for recruitment based on observation of 0.11 30-day-old ducklings produced per nesting female. Lastly, duckling survival probability was lowest shortly after hatch, as found for other species of ducklings (Grand and Flint 1996, Dzus and Clark 1997, Guyn and Clark 1999, Gendron and Clark 2002). However, in 2000, the daily survivorship function was a quadratic trend with age; and we suggest that this decrease in survival with advancing age was attributable to a complex combination of factors, such as decreasing food resources, disease, predation, adverse weather late in the brood-rearing season, and energetic constraints faced by developing ducklings (Bourgeois and Threlfall 1982, Mendenhall and Milne 1985, Brown and Fredrickson 1986, Mitcham and Wobeser 1988, Brown and Fredrickson 1989).

Proximate cause of mortality.—Gull populations in the Prairie Parkland in Canada have grown ~11% since 1967 (Downes and Collins 2003). Furthermore, a large (~13,000 pairs) population of California and Ring-billed gulls nested at Redberry Lake during our study (Redberry Lake Pelican Project unpubl. data); both species prey on young ducklings (J. J. Traylor pers. obs.). Gulls at Redberry Lake disperse from colonies to loaf on island shorelines around modal dates of scoter hatch and appear to consume a high proportion of ducklings as they enter the water with females within a day of hatch (Kehoe 1989, present study). Although scoter ducklings show specific adaptations, such as diving and crèching, which may reduce gull predation (Brown and Brown 1981), we suspect that high predation of scoter ducklings by nesting gulls overwhelms the potential for recruitment of locally produced scoter ducklings (Mendenhall and Milne 1985). Thus, breeding islands may currently function as ecological traps (Dwernychuk and Boag 1972).

High salinity levels can be fatal to young ducklings, because salt glands may not function properly in neonates until after a week of exposure (Mitcham and Wobeser 1988), even for marine species such as Common Eiders (*Somateria mollissima*) (DeVink et al. 2005). Redberry Lake is saline, and highest densities of

broods are often located near freshwater sources (i.e. streams), which suggests that access to freshwater may be crucial for duckling survival. Salinity may cause mortality directly or indirectly by compromising immune response and ability of ducklings to handle adverse weather and predation attempts (Swennen 1989). Elevated salinity levels also may influence food availability (i.e. abundance of amphipods; Hammer et al. 1990) for ducklings and may compromise proper feeding and nutrient assimilation. Thus, we hypothesize that salinity at Redberry Lake may play a central role in diminished duckling survival as compared with other species, by amplifying effects on ducklings of inanition, internal parasite loads, disease, weather, hypothermia, and predation probability.

Influences on survival.—Duckling survival declined with advancing hatch date, with additional declines related to duckling condition. Diminished survival of ducklings that hatch later in the nesting season has been observed in other studies (Rotella and Ratti 1992, Dzus and Clark 1998, Guyn and Clark 1999) and may be an outcome of increased predation (Grand and Flint 1996), declines in wetland quality and food resources (Rotella and Ratti 1992, 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 lakes, such as Redberry Lake. Still, scoter ducklings fledge in early October, so we believe that declining food resources (Brown and Fredrickson 1986), adverse weather conditions, and perhaps increasing internal parasite loads and diseases (Bourgeois and Threlfall 1982, Mendenhall and Milne 1985) may reduce survival of ducklings hatched later.

Our results suggest strong effects of duckling body size and condition on subsequent probability of duckling survival. Pelayo and Clark (2003) found that ducklings from larger eggs (i.e. larger, better-conditioned ducklings) had higher survival probabilities than those hatching from smaller eggs (Dawson and Clark 1996, 2000; Christensen 1999), though results were inconsistent in other species (Smith et al. 1993, Williams et al. 1993). Larger offspring are believed 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). Additionally, we found that the influence of duckling condition on survival was confounded by an interaction with hatch date. Specifically, ducklings in better condition survived better than those in poor condition, and this disparity increased as hatch date progressed. Perhaps larger or better-conditioned ducklings were better able to survive as environmental conditions deteriorated later in the summer. For example, Anderson and Alisauskas (2001) found that larger King Eider (*S. spectabilis*) ducklings show better locomotor performance than smaller ducklings. Ultimately, high mortality of small individuals may be related to small body size and lower energy reserves at hatch (Pelayo and Clark 2003).

We found that likelihood of survival by scoter ducklings was related to social structure of broods. Small broods showed the lowest survival, though predators presumably should select larger broods to maximize foraging efficiency (Mendenhall and Milne 1985, Stephens and Krebs 1986). We suspect that intense gull predation shortly after hatch makes large brood size adaptive (Kehoe 1989). Larger brood size may increase likelihood of individual duckling survival through (1) the dilution effect (i.e. larger brood size reduces the risk of predation per young) or (2) rapidly detecting and confusing predators (Eadie et al. 1988, Bustnes and Erikstad 1991; see Johnson et al. 1992). Finally, smaller broods may suffer higher mortality from reduced female attentiveness correlated with reduced investment and relatively lower fitness (Eadie et al. 1988, Dzús and Clark 1997).

Here, larger ducklings (i.e. larger eggs) and broods (i.e. clutch size) survived better. If a tradeoff exists between egg size and clutch size, imposed by an upper limit to how many clutch nutrients can be produced (Rohwer 1988, Blums et al. 2002), then there may be an optimal clutch-size and egg-size relationship in conjunction with duckling survival. Blums et al. (2002)

found a negative relationship between brood size or clutch size and duckling size. However, we did not detect any relationships between brood size or clutch size and duckling size or egg size while controlling for female size and condition, which suggests that egg production is not limited by nutrient availability in this population of scoters.

Although scoter ducklings are believed to have a high tolerance for inclement weather (Koskimies and Lahti 1964), duckling survival showed a strong negative relationship with inclement weather. Ducklings likely require greater energy reserves to endure periods of severe weather, when food intake declines and energy reserves are depleted (Johnson et al. 1992, Pelayo and Clark 2003). Adverse 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 (Mendenhall and Milne 1985, Johnson et al. 1992, Korschgen et al. 1996). Further, predation may show an important interplay with inclement weather where high winds can (1) decrease duckling survival by improving foraging gulls' maneuverability and chances of successful attacks (Gilchrist et al. 1998) and (2) force high densities of broods into calm, but small, inlets where gull predation can be high (Johnson et al. 1992). Interestingly, other studies did not detect consistent effects of poor weather (Blums et al. 2002, Pelayo and Clark 2003), which may be related to these sites having lower predator densities than at Redberry Lake. Redberry Lake is ~10 km in diameter, and high winds (i.e. 60–70 km h⁻¹) 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 and others (Arnold et al. 1995, Gendron and Clark 2002). We found that larger females in poorer condition had higher duckling survival, though estimates were imprecise. Structurally larger females may increase duckling survival by displacing subordinate females from appropriate brood-rearing habitats or physically defending offspring against predation attempts. Body condition may be important because females endure energetic constraints during brood

rearing by defending broods and increasing vigilance for predators, which decreases time for self maintenance (Bustnes and Erikstad 1991). Moreover, females in poor condition may show a proclivity to abandon broods (Eadie et al. 1988, Kehoe 1989), which in turn can suffer greater attrition from predators and adverse weather immediately after abandonment (Talent et al. 1983, Bustnes and Erikstad 1991). Our result contradicts these findings. However, we hypothesize that a negative relationship between female condition and duckling survival resulted in part from poor-condition females abandoning young after hatch; such ducklings often joined larger amalgamated broods in which survival probability was higher as compared with that of maternal broods diminished by predation (Kehoe 1989, Traylor et al. 2004b). Finally, sex of ducklings, beyond sex-related differences in duckling size, was not important to survival (Dawson and Clark 1996). Our results suggest that probability of survival by scoter ducklings at Redberry Lake is a demonstrably complex function of a variety of extrinsic and intrinsic factors. The influence of extrinsic factors is believed to be more important than that of intrinsic factors on duckling survival (Blums et al. 2002), though our study also underscores the importance of intrinsic factors (i.e. duckling size, duckling condition, and brood size).

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