



## KING EIDER (*SOMATERIA SPECTABILIS*) BROOD ECOLOGY: CORRELATES OF DUCKLING SURVIVAL

KATHERINE R. MEHL<sup>1,3</sup> AND RAY T. ALISAUSKAS<sup>2</sup>

<sup>1</sup>University of Saskatchewan, Department of Biology, 112 Science Place, Saskatoon SK S7N 5E2, Canada; and

<sup>2</sup>Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, 115 Perimeter Road,  
Saskatoon SK S7N 0X4, Canada

**ABSTRACT.**—Events during duckling growth can influence waterfowl population dynamics. To gain insight into King Eider (*Somateria spectabilis*) brood ecology, we monitored 111 and 46 individually marked ducklings from broods of 23 and 11 radiomarked King Eiders during 2000 and 2001, respectively. We used capture–mark–resight data to model apparent survival of King Eider ducklings and broods, and multistratum analysis to estimate probabilities of (1) movement among habitats and (2) apparent survival of ducklings that used various habitats. In addition, we recorded length of stay for 7 and 18 radiomarked females with failed nesting attempts during 2000 and 2001, respectively. Complete loss of individual broods accounted for 84% of all duckling mortality (106 of 126 mortalities), with most brood loss (74%; 17 of 23 broods lost) within the first two days after hatch. Estimated apparent survival of ducklings to 24 days of age was 0.10 (95% CI: 0.05 to 0.15). Apparent survival of broods was estimated to be 0.31 (95% CI: 0.13 to 0.50). Our data suggested an interaction between female size and hatch date, whereby larger females whose ducklings also hatched earlier raised more ducklings than either small females or those with ducklings that hatched later. Overland brood movements  $\geq 1$  km occurred in both years, and survival was greatest for ducklings on smaller ponds away from the central nesting area at Karrak Lake, Nunavut. Females that experienced nest failure and total brood loss left the study area earlier than females with surviving ducklings. Received 22 December 2004, accepted 4 June 2006.

**Key words:** brood, duckling, habitat use, King Eider, *Somateria spectabilis*, survival.

Écologie d'élevage des couvées de *Somateria spectabilis* : Corrélations avec la survie des canetons

**RÉSUMÉ.**—Les événements survenant au cours de la croissance des canetons peuvent influencer la dynamique des populations de sauvagine. Afin d'en savoir plus sur l'écologie d'élevage des couvées chez l'Eider à tête grise (*Somateria spectabilis*), nous avons suivi 111 et 46 canetons marqués individuellement et appartenant à 23 et 11 femelles dotées d'émetteurs en 2000 et 2001, respectivement. Nous avons utilisé des données de capture–marquage–réobservation afin de modéliser la survie apparente des canetons et des couvées d'Eider à tête grise. Une analyse en multistrates a aussi été réalisée pour estimer les probabilités (1) de mouvement entre les habitats et (2) de survie apparente des canetons ayant utilisé différents habitats. De plus, nous avons enregistré la durée de séjour de 7 et 18 femelles dotées d'émetteurs et ayant échoué la nidification en 2000 et 2001, respectivement. La perte totale des couvées comptait pour 84% de toutes les mortalités de canetons (106 des 126 mortalités), la plupart survenant dans les deux premiers jours après l'éclosion (74%; 17 des 23 couvées disparues). La

<sup>3</sup>Present address: Ducks Unlimited Canada, 6 Bruce Street, Mount Pearl, Newfoundland A1K 4T3, Canada.  
E-mail: kr\_mehl@ducks.ca

survie apparente des canetons jusqu'à l'âge de 24 jours a été estimée à 0.10 (95% CI: 0.05 à 0.15). La survie apparente des couvées a été évaluée à 0.31 (95% CI: 0.13 à 0.50). Nos données suggèrent une relation entre la taille de la femelle et la date d'éclosion : les femelles plus grosses dont les canetons ont éclos tôt en saison ont élevé plus de canetons que les femelles plus petites ou dont les canetons ont éclos plus tard. Les déplacements terrestres des couvées sur 1 km se sont produits lors des deux années. La survie était plus grande pour les canetons sur les étangs plus petits, situés loin de l'aire principale de nidification du lac Karrak, au Nunavut. Les femelles ayant échoué la nidification et celles ayant perdu la totalité de leurs couvées ont quitté l'aire d'étude plus tôt que les femelles dont les canetons ont survécu.

ESTIMATION OF TRANSITION probabilities between life-cycle stages is essential for a good understanding of population dynamics in free-ranging animals. Adult survival constitutes the greatest proportion of annual rate of population change in long-lived species (Rockwell et al. 1997); adult survival, however, is relatively stable compared with annual variation in production of young and recruitment (Coulson 1984). In extreme cases, changes in population growth rate can result entirely from changes in recruitment (Coulson 1984, Cooch et al. 2001).

Knowledge of survival, movements, and habitat requirements of waterfowl broods is essential for understanding the importance of duckling ecology as a component of recruitment (Johnson et al. 1992, Sedinger 1992). After nest success, duckling survival is considered the most limiting factor on recruitment (Johnson et al. 1992). Several abiotic and biotic factors are correlated with prefledgling survival of precocial young, including weather (Mendenhall 1979), hatch date (Cooke and Findlay 1982), dispersal distance of broods (Ball et al. 1975, Sedinger 1992), and attributes of both offspring and females such as size and condition (Afton and Paulus 1992, Christensen 1999). Previous research focused on single-factor relationships with survival and was restricted to pooling survival estimates from multiple weeks to establish composite estimates for the brood-rearing period (Dzus and Clark 1997, Flint et al. 1998). More recent, capture-mark-resight (CMR) methods permit greater flexibility when modeling survival estimates. Specifically, CMR techniques allow partitioning variation in survival that can be attributed to numerous potential correlates (White and Burnham 1999).

Our objectives were to use CMR techniques and radiotelemetry to estimate probabilities of movement and survival by King Eider

(*Somateria spectabilis*) ducklings and estimate ecological variables that may influence those probabilities. We gained insight about the importance of brood-rearing habitats to brood survival and, in turn, the influence of brood loss on residency in such habitats by females.

#### METHODS

*Study area.*—The study was conducted on Karrak Lake and Adventure Lake and on surrounding freshwater habitats. The study area (67°14'N, 100°15'W) was ~60 km south of Queen Maud Gulf, Nunavut, Canada. Karrak Lake and Adventure Lake support the highest known density of nesting King Eiders (Kellett and Alisauskas 1997). Karrak Lake averages ~1.2 m in depth, with an area of 16.1 km<sup>2</sup>, and contains 2.5 km<sup>2</sup> of islands of various sizes. Adventure Lake, ~300 m east of Karrak Lake, averages ~2.5 m in depth, is 8.8 km<sup>2</sup> in size, and contains 0.2 km<sup>2</sup> of islands (Kellett and Alisauskas 2000). Surrounding wetland habitats and lakes vary in size, but all are smaller than either Karrak or Adventure Lake. An automatic weather station at the Karrak Lake research camp recorded daily maximum and minimum ambient temperatures, precipitation, and wind speed.

*Nest search and trapping.*—We systematically searched islands within Karrak Lake and Adventure Lake for King Eider nests beginning in mid-June, 2000 and 2001. Islands were searched two or three times to increase the probability of finding most nests. We calculated nest initiation date (i.e., date the first egg was laid in a nest) by backdating from known laying dates or from estimated incubation stages by candling eggs (Weller 1956), assuming an incubation period of 23 days (Parmelee et al. 1967) and a laying interval of one egg per day (Lamothe 1973).

We trapped nesting female King Eiders four to seven days before predicted hatch dates (early to mid-July) by laying mist nets over incubating females or by self-triggered bow nets. We marked females with standard metal leg bands, and weighed each with a Pesola scale ( $\pm 10$  g). We recorded (by the same observer, twice for each female) head and tarsus lengths using dial calipers ( $\pm 1.0$  mm), and wing chord using a flat ruler ( $\pm 1.0$  mm; Dzubin and Cooch 1993). We attached subcutaneous anchor-mounted transmitters (18 g, 30-day life, 7 km range; Advanced Telemetry Systems, Isanti, Minnesota; Mauser and Jarvis 1991) to a subset of captured females ( $n = 30$ , every 2nd capture in 2000;  $n = 29$ , every 3rd capture in 2001) and attached uniquely colored nasal tags using surgical sutures through the nares. Dissolving sutures permitted nasal tags to fall away before winter. Before releasing the females, we switched all King Eider eggs in nests with an equal number of color-dyed, non-fertile chicken eggs and administered 1–1.5 mL Propofol in tarsal veins of females to reduce nest abandonment (Machin and Caulkett 2000). We placed all eider eggs (including known inviable ones) that were removed from nests into air-circulating cabinet incubators at camp, with individual compartments for each egg; all eggs from a clutch were artificially incubated to simulate what the female would incubate naturally. Hatching success of artificially incubated eggs was  $>95\%$ , with most failures attributable to known inviability before placement in incubators. Artificial incubation of King Eider eggs enabled us to mark and record measurements for the complete brood of each radiomarked female before departure from the nest. Clutches were kept in brooders until ducklings were dry. We weighed dry ducklings using a digital scale ( $\pm 0.1$  g) and recorded head and tarsus lengths (mean of two measurements by the same observer using digital calipers;  $\pm 0.5$  mm; Dzubin and Cooch 1993). We marked each with a plasticine leg band (Blums et al. 1994) and a uniquely colored nape-marker (Pelayo 2001). Finally, we returned marked ducklings and any inviable King Eider eggs to their original nests, after removing chicken eggs and loosely wrapping ducklings in a paper-towel envelope to encourage them to remain in nests until females returned (Korschgen et al. 1996). Nape-markers consisted of brass safety pins (size 0) with unique combinations of colored tabs. Colored

tabs consisted of shorebird leg-band blanks (A.C. Hughes, Middlesex, United Kingdom) bent in half over the fixed portion of the safety pin and glued in place using clear polyvinyl chloride (PVC) cement.

Nests of six radiomarked females were depredated in 2000, and one nest was abandoned before ducklings could be returned to nests. We divided ducklings from 6 of the 7 above failed nests among 4 different radiomarked females whose broods had hatched on the same day, artificially increasing brood size for 4 of 23 radiomarked females. Brood enlargements consisted of 3, 5, 6, and 7 ducklings added, resulting in brood sizes of 5, 10, 11, and 11, respectively. In 2001, 12 nests were depredated and 6 radiomarked females abandoned before hatch. Because remaining broods were few, we did not manipulate brood size of 11 radiomarked females that did not abandon broods in 2001.

We located radiomarked females once every two days over a 24-day period and recorded total number of adult female King Eiders present, number of ducklings, corresponding color codes of nape tags, status of brood (amalgamated or not), and habitat type—pond ( $<1$  km<sup>2</sup>), lake ( $>1$  km<sup>2</sup>), or river. To minimize observer disturbance to broods that would lead to possible gull predation, we did not attempt to record nape tag colors when foraging gulls (*Larus* spp.) were nearby.

#### STATISTICAL ANALYSES

*Covariates for survival analyses.*—We used principal component analysis (PCA; PROC PRINCOMP, SAS; SAS Institute 1996) of the correlation matrix of mean measurements for each bird to establish an index of structural size (first principal component [PC1]). We regressed body weight on structural size (PC1<sup>adult</sup>) and incubation stage at capture (PROC GLM) to estimate (1) adult female body weight corrected for size and incubation stage and (2) duckling weight corrected for duckling size (PC1<sup>duckling</sup>) and hatch date (Alisauskas and Ankney 1990). We tested for brood-size variation among years and hatch dates (PROC GLM). We assessed correlations of duckling size and condition with female size (PROC CORR). We also used PCA to derive indices of weather (PC1<sup>weather</sup>, PC2<sup>weather</sup>) from the correlation matrix of mean maximum relative humidity, minimum ambient temperature,

and maximum wind speed for the first seven days after hatch.

We considered the following effects as sources of variation in survival: (1) year, (2) hatch date (adjusted for median hatch of the colony in a given year), (3) brood size, (4) natal female size and (5) condition, (6) duckling size and (7) condition, (8, 9) PC scores of weather, and (10) distance traveled from the nest site during the first week after hatch. In addition, we investigated (11) the presence of an optimal hatch date and (12) brood size using quadratic relationships of these covariates with survival and investigated pseudothreshold relationships, whereby estimates of offspring survival asymptotically approached 100% (see Franklin et al. 2000) among (13) hatch date, (14) brood size, (15) female size, and (16) duckling size. We assessed correlations of female size and hatch date, using hatch date compared with median hatch date among years in our analyses. Because of small sample size (23 and 11 broods in 2000 and 2001, respectively), we did not consider individual level covariates in models of brood survival.

*Modeling apparent survival.*—We estimated apparent survival ( $\hat{\phi}_i$ ) and recapture probability ( $\hat{p}_i$ ) of marked ducklings for each two-day interval ( $i$ ) using Cormack-Jolly-Seber (CJS) models in MARK (White and Burnham 1999). We were unable to obtain estimates of true survival ( $\hat{S}_i$ ), because we could not locate all ducklings at specific intervals owing to early transmitter failure and because we did not record all nape tag colors in the presence of foraging gulls. Therefore,  $\hat{\phi}_i$  represents the product of true survival and fidelity to our study area during brood rearing. We confirmed identities of females with failed transmitters by observing nasal-tag combinations. Fates among brood-mates are likely not independent (e.g., complete brood loss and brood survival), so we also modeled brood survival for all radiomarked females. Nape-markers were placed too low on necks of ducklings from two broods ( $n = 1$  brood year<sup>-1</sup>), precluding their identification, so these were excluded from analyses. Our survival estimates were not affected by transmitter failure or lack of recording nape colors when foraging gulls were present, because these factors did not prevent detection in outlying areas.

We tested model fit using the global time-dependence model ( $\hat{\phi}_i, \hat{p}_i$ ) and the parametric bootstrap method in MARK (White and

Burnham 1999). We adjusted the variance inflation factor ( $\hat{c}$ ) to account for lack of model fit by dividing the deviance of the most general model by the mean deviance from 1,000 bootstrap iterations (Burnham and Anderson 2002). For estimates of duckling survival, we assumed that  $\hat{c}$  accounts for the lack of independence among brood-mates. Model selection was based on quasi-likelihood Akaike's Information Criterion (QAIC<sub>c</sub>) corrected for small sample size, lack of fit, and overdispersion (Akaike 1985, Burnham and Anderson 2002).

In addition to our time dependence model, we considered models with constant resighting and survival probabilities. We chose the best model without covariates and used this model to investigate age trends with survival. Age trends included survival modeled as (1) a linear function and (2) the natural log of a linear relationship (pseudothreshold model) of duckling age, whereby offspring survival increased asymptotically with age. Proceeding with the best model, we estimated slopes ( $\beta_j$ ) between each covariate and survival. When the 95% confidence intervals (CI) included zero, precision was judged to be poor and such covariates were excluded from subsequent models. We chose this approach because of small sample size and the desire to reduce the number of parameter estimates. After testing for interactions of covariates, we determined that the following six covariates were most important (i.e., 95% CI did not encompass zero) to survival of ducklings that remained with radiomarked females: (1) hatch date, (2) pseudothreshold hatch date, (3) duckling size, (4) pseudothreshold duckling size, (5) female size, and (6) pseudothreshold female size. Model-averaged estimates of  $\hat{\phi}_i$  and  $\hat{p}_i$  were calculated for the study period to account for model uncertainty (Burnham and Anderson 2002). Apparent duckling survival up to 24 days of age was defined as the product of the 11 model-averaged estimates for two-day intervals between 12 observational periods. Variances for model-averaged estimates were calculated using the delta method to account for covariance between consecutive survival estimates. Parameter estimates represent the maximum likelihood and corresponding 95% CI based on the sine (identity matrices) and logit-link function (non-identity matrices) in MARK (White and Burnham 1999); MARK scaled  $([x_i - \bar{x}]/SD)$  covariates automatically.

*Survival and movements among habitats.*—We used multistratum models (Lebreton et al. 1999) to assess how survival changed in response to dispersal and habitat use. Encounters were classified as either “K” if on Karrak Lake or Adventure Lake where most ducklings were hatched, or as “O” if on any other habitat such as lakes, ponds, or rivers away from Karrak Lake or Adventure Lake. Probabilities estimated from multistratum models included (1) apparent survival,  $\phi_{ij}^r$ ; (2) resighting probability,  $p_{ij}^r$ ; and (3) conditional transition probability,  $\Psi_i^{rs}$  (Brownie et al. 1993, Nichols et al. 1994).

We tested goodness-of-fit of habitat models using U-CARE (Pradel et al. 2003) and calculated QAIC<sub>c</sub> from AIC<sub>c</sub> to correct for small sample size using a variance inflation factor

$$\hat{c} = \frac{\chi^2}{df}$$

to correct for overdispersion (Akaike 1985, Burnham and Anderson 2002). Model selection proceeded as above, by first adding time constraints to resighting probabilities, then transition probabilities, and lastly time constraints to survival without covariates.

RESULTS

*Size and amalgamation of broods.*—We marked 111 and 46 ducklings from nests of 23 and 11 radiomarked King Eiders in 2000 and 2001,

respectively. We encountered marked ducklings 252 and 128 times and marked broods 86 and 50 times in 2000 and 2001, respectively. We also encountered radiomarked females following brood loss 119 and 54 times and radiomarked females with failed nesting attempts 30 and 138 times in 2000 and 2001, respectively.

Brood size at hatch did not vary between years or hatch dates ( $F = 1.77$ ,  $df = 11$  and  $32$ ,  $P = 0.13$ ). Including artificially enlarged broods, these ranged from 3 to 11 in 2000 and from 3 to 6 in 2001. Median hatch date was two days earlier in 2001 ( $n = 91$  nests, 18 July) than in 2000 ( $n = 57$  nests, 20 July). Marked ducklings represented mostly early and mid-hatched nests (Fig. 1).

Brood amalgamations occurred within two days of hatch ( $n = 5$  broods in 2000;  $n = 3$  broods in 2001), with a mean of 3 females and 9 ducklings in 2000 and 4 females and 7 ducklings in 2001. Amalgamated broods ranged from 7 ducklings and 2 females to as large as 29 ducklings and 10 females. Amalgamations of ducklings appeared to remain stable, though females with brood loss (13 of 34 females) and those with failed nesting attempts (10 of 25 females) appeared to often join broods temporarily. We also observed temporary brood abandonment, in which a female that had hatched three young was observed alone four days after hatch and was later observed with three young, only one of which hatched from her nest. One other marked duckling from this female was observed in a separate brood with a nonmarked

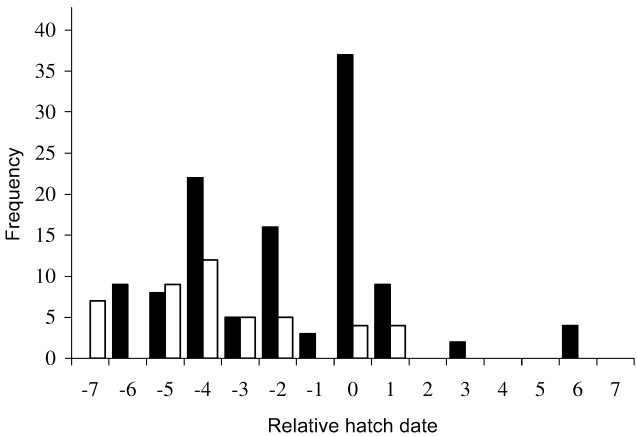


FIG. 1. Frequency distribution of relative hatch dates of King Eider broods marked on Karrak and Adventure lakes, Nunavut, during 2000 (solid bars;  $n = 23$  broods) and 2001 (open bars;  $n = 11$  broods). Hatch dates are relative to the median hatch date of the colony for a given year.



female. We never observed more than one marked duckling in unmarked broods.

*Covariates of duckling survival.*—Our index of duckling size ( $PC1^{duckling}$ ) accounted for 73% of variation in body measures, with  $PC1$  loadings of 0.86 for both head and tarsus. Adult female size ( $PC1^{adult}$ ) accounted for 66% of the variation in female body measures, with loadings of 0.80, 0.78, and 0.84 for head length, tarsus, and wing, respectively. When corrected for hatch date and incubation stage at capture, larger duckling size was positively related to weight of both ducklings ( $F = 15.82$ ,  $df = 2$  and  $156$ ,  $r^2 = 0.17$ ,  $P < 0.01$ ) and adults ( $F = 15.50$ ,  $df = 2$  and  $33$ ,  $r^2 = 0.50$ ,  $P < 0.01$ ). Adult female size was correlated with size ( $r = 0.36$ ,  $P < 0.01$ ,  $n = 157$ ) and condition ( $r = 0.17$ ,  $P = 0.03$ ,  $n = 157$ ) of ducklings at hatch, though larger females did not nest earlier ( $r = 0.04$ ,  $P > 0.84$ ,  $n = 34$ ).

Weather ( $PC1^{weather}$ ) accounted for 57% of the variation in maximum relative humidity,

minimum ambient temperature, and maximum wind speed for the first week of hatch, with respective loadings of  $-0.82$ ,  $0.90$ , and  $0.49$ . Positive  $PC1^{weather}$  scores represented drier, warmer, and windier days, whereas negative scores represented damper, cooler, and calmer days.  $PC2^{weather}$  accounted for an additional 31% of total variation in weather data (i.e., 88% cumulative variation for  $PC1^{weather}$  and  $PC2^{weather}$ ), with loadings of  $0.43$ ,  $-0.08$ , and  $0.86$  for maximum relative humidity, minimum temperature, and maximum wind speed, respectively. Thus, positive  $PC2^{weather}$  scores represented damp, windy days, whereas negative scores represented dry, calm days.

*Survival of ducklings and broods.*—We considered 40 candidate models ( $\hat{c} = 1.34$ ) for ducklings accompanied by radiomarked females (Table 1) and 30 models ( $\hat{c} = 1.35$ ) for analyses of brood survival (Table 2). We also considered 17

TABLE 1. Best 14 of 40 candidate models of apparent survival ( $\phi$ ) and resighting probability ( $p$ ) of 111 and 46 King Eider ducklings at Karrak Lake, Nunavut, in 2000 and 2001, respectively. Models are based on observations of marked ducklings brooded by radiomarked females. Parameter estimates included year and age effects, where time varied annually and with age ( $yr,t$ ), linearly with age ( $T$ ), in a pseudothreshold relationship with age ( $T_{ln}$ ), and no time or year variation ( $\cdot$ ). Model covariates included: hatch date ( $hd$ ), brood size ( $bs$ ), duckling body size ( $ds$ ), duckling condition ( $dc$ ), female size ( $fs$ ) and female condition ( $fc$ ), distance moved from the nest during the first week ( $dist$ ), and principal components of weather during the first week after hatch ( $w1$ ,  $w2$ ). Hatch date, distance moved, brood size, and female and duckling size were also entered as a pseudothreshold relationship ( $X_{ln}$ ), and hatch date and brood size in a quadratic relationship ( $X_{TT}$ ). Models are ranked in accordance with  $QAIC_c$  values and are indicated as additive models (+) or models with single and interactive effects (\*).

Model	$\Delta QAIC_c^a$	$QAIC_c$ weights	Number of estimable parameters	QDeviance
1 $\phi(\cdot, T_{ln} fs_{ln} * hd_{ln}) p(yr,t)$	0.00	0.57	23	578.84
2 $\phi(\cdot, T_{ln} + fs_{ln} * hd_{ln} + dc) p(yr,t)$	0.96	0.36	24	577.55
3 $\phi(\cdot, T_{ln} fs_{ln} + hd_{ln}) p(yr,t)$	4.32	0.07	22	585.39
4 $\phi(\cdot, T_{ln} + fs_{ln}) p(yr,t)$	12.69	0.00	21	595.98
5 $\phi(\cdot, T_{ln} + fs) p(yr,t)$	12.88	0.00	21	596.17
6 $\phi(\cdot, T_{ln} + fs_{ln} + dc) p(yr,t)$	13.63	0.00	22	594.69
7 $\phi(\cdot, T_{ln} * fs) p(yr,t)$	14.61	0.00	22	595.68
8 $\phi(\cdot, T_{ln} + fs_{ln} * dc) p(yr,t)$	15.51	0.00	23	594.35
9 $\phi(\cdot, T_{ln} + hd_{ln}) p(yr,t)$	16.11	0.00	21	599.39
10 $\phi(\cdot, T_{ln} + hd_{ln} * dc) p(yr,t)$	17.68	0.00	23	596.52
11 $\phi(\cdot, T_{ln} + hd) p(yr,t)$	18.14	0.00	21	601.42
12 $\phi(\cdot, T_{ln} * hd) p(yr,t)$	20.15	0.00	22	601.22
13 $\phi(\cdot, T_{ln} + dist) p(yr,t)$	24.82	0.00	21	608.10
14 $\phi(\cdot, T_{ln} * ds_{ln}) p(yr,t)$	25.28	0.00	22	606.35

<sup>a</sup>Lowest  $QAIC_c$  value = 627.52.

TABLE 2. Best 14 of 30 candidate models of apparent survival ( $\phi$ ) and resighting probability ( $p$ ) of 23 and 11 King Eider broods at Karrak Lake, Nunavut, in 2000 and 2001, respectively. Models are based on observations of marked broods with radiomarked females. Parameter estimates included year and age effects, where time varied annually and with age (yr,t), linearly with age (T), in a pseudothreshold relationship with age ( $T_{ln}$ ), and no time or year variation (.). Model covariates included: hatch date (hd), brood size (bs), female size (fs) and female condition (fc), distance moved from the nest during the first week (dist), and principal components of weather during the first week after hatch (w1, w2). Hatch date, distance moved, brood size, and female size were also entered as a pseudothreshold relationship ( $X_{ln}$ ), and hatch date and brood size in a quadratic relationship ( $X_{TT}$ ). Models are ranked in accordance with QAIC<sub>c</sub> values and are indicated as additive models (+) or models with single and interactive effects (\*).

Model	$\Delta QAIC_c^a$	QAIC <sub>c</sub> weights	Number of estimable parameters	QDeviance
1 $\phi(.,T_{ln} + fs) p(.,.)$	0.00	0.10	4	236.06
2 $\phi(.,T_{ln}) p(.,.)$	0.05	0.10	3	238.21
3 $\phi(.,T_{ln} + fs_{ln}) p(.,.)$	0.56	0.08	4	236.62
4 $\phi(.,T_{ln} + hd_{ln}) p(.,.)$	0.89	0.07	4	236.95
5 $\phi(.,T_{ln} + hd) p(.,.)$	1.19	0.06	4	237.25
6 $\phi(.,t) p(.,.)$	1.39	0.05	7	231.01
7 $\phi(.,T_{ln} + fc) p(.,.)$	1.40	0.05	4	237.46
8 $\phi(.,T_{ln} + w2) p(.,.)$	1.51	0.05	4	237.57
9 $\phi(.,T_{ln} * w2) p(.,.)$	1.58	0.05	5	235.52
10 $\phi(.,T_{ln} * fs) p(.,.)$	1.92	0.04	5	235.86
11 $\phi(.,T_{ln} + hd_{TT}) p(.,.)$	2.10	0.04	4	238.17
12 $\phi(.,T_{ln} + bs) p(.,.)$	2.11	0.04	4	238.18
13 $\phi(.,T_{ln} + bs_{ln}) p(.,.)$	2.12	0.04	4	238.19
14 $\phi(.,T_{ln} + bs_{TT}) p(.,.)$	2.12	0.04	4	238.19

<sup>a</sup>Lowest QAIC<sub>c</sub> value = 244.30.

multistratum models for estimation of movement and survival probabilities between habitat types ( $\hat{c} = 1.51$ ; Table 3). Model results suggested that estimates of both duckling and brood survival were similar among years. All observed predation on ducklings and full broods was by gulls. Brood loss was detected in 65% of 34 broods and accounted for 84% of 126 apparent duckling mortalities. Most brood loss (74%; 17 of 23) occurred within two days of hatch (Fig. 2). No mortality occurred after 14 days of age, but, owing to high mortality of very young ducklings, composite duckling survival to 24 days of age was estimated as 0.10 (95% CI: 0.05 to 0.15), and 0.31 (95% CI: 0.13 to 0.50) for broods. We observed six ducklings that were abandoned by putative mothers but fostered by other females with broods. In addition, we resighted four marked ducklings ( $n = 3$  broods) that had joined other broods but whose putative mothers continued to accompany siblings of the fostered ducklings.

Resighting probability of ducklings ( $\hat{p}^d$ ) varied between years and among duckling ages. For ducklings that remained with radiomarked females,  $\hat{p}^d = 0.63$  in 2000 (95% CI: 0.42 to 0.80) and  $\hat{p}^d = 0.75$  in 2001 (95% CI: 0.53 to 0.92). Resighting probability of broods was similar regardless of brood age or year,  $\hat{p}^b = 0.76$  (95% CI: 0.66 to 0.83).

The best model(s) (QAIC<sub>c</sub> weight  $\approx 1.0$ ) for duckling survival included additive effects of female size and hatch date and interactions between these covariates (Table 1). In general, ducklings brooded by larger females that hatched earlier tended to have higher survival (Fig. 3). Also, ducklings that hatched in better condition tended to survive better ( $\Delta QAIC_c < 2$ ; Table 1); however, model-averaged estimates were less precise ( $\hat{\beta}_{\text{ducklingcondition}} = 0.06$ , 95% CI:  $-0.15$  to  $0.28$ ), so we considered this a secondary influence. Brood models showed some support for female size and hatch date ( $\Delta QAIC_c < 2$ ;

TABLE 3. Top 9 of 17 candidate models of apparent survival ( $\phi$ ), resighting ( $p$ ), and movement probability ( $\psi$ ) of King Eider broods that moved from Karrak Lake, the primary brood area, to other lakes, ponds, or rivers away from Karrak Lake. Models are based on observations of marked broods resighted with radiomarked females at Karrak Lake, Nunavut, in 2000 and 2001. Parameter estimates included year and full-time effects where time varied annually and with duckling age ( $yr,t$ ), linearly with time ( $T$ ), in a pseudothreshold relationship with time ( $T_{ln}$ ), and no time or year variation ( $\cdot$ ). Apparent survival ( $\phi$ ) and  $p$  were estimated for ducklings observed on Karrak Lake (K) or on other habitats (O) and movement of ducklings from Karrak Lake to other habitats (K-O) or movements back to Karrak Lake (O-K). Models are ranked in accordance QAIC<sub>c</sub> values and are denoted as additive models (+) or models with interaction (\*).

Model	$\Delta QAIC_c^a$	QAIC <sub>c</sub> weights	Number of parameters	QDeviance
1 $\phi^{K_i(T_{ln})}\phi^{O(\cdot,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	0.00	0.52	30	197.93
2 $\phi^{K_i(t)}\phi^{O(\cdot,t)}p^K(yr,t)p^O(yr,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	1.30	0.27	34	189.93
3 $\phi^{K_i(\cdot,T)}\phi^{O(yr,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	3.46	0.09	35	189.72
4 $\phi^{K_i(\cdot,T)}\phi^{O(\cdot,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	4.05	0.07	30	201.98
5 $\phi^K(yr,t)\phi^{O(yr,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	7.09	0.01	38	186.22
6 $\phi^K(yr,t)\phi^{O(yr,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,2000t,2001\cdot)$	7.09	0.01	38	186.22
7 $\phi^{K_i(\cdot,T_{ln})}\phi^{O(\cdot,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	7.95	0.01	30	205.88
8 $\phi^{K_i(\cdot,t)}\phi^{O(\cdot,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	8.79	0.01	34	197.41
9 $\phi^{K_i(\cdot,T_{ln})}\phi^{O(\cdot,t)}p^K(yr,t)p^O(\cdot,t)\psi^{K\rightarrow O}(yr,t)\psi^{O\rightarrow K}(yr,t)$	9.19	0.01	31	204.81

<sup>a</sup>Lowest QAIC<sub>c</sub> value = 611.84.

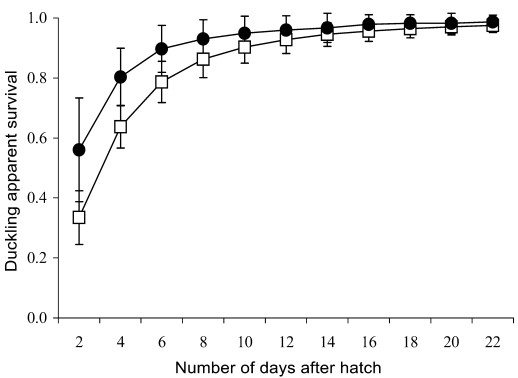


FIG. 2. Estimates of daily apparent survival and 95% CI for King Eider ducklings and broods marked on Karrak Lake and Adventure Lake, Nunavut, during July and August, 2000 and 2001. Values were calculated using the logit-link function and are the weighted averages based on candidate models. Averages were weighted according to QAIC<sub>c</sub> values. Closed circles = brood survival, and open squares = duckling survival for ducklings that remained with radiomarked females.

Table 2); however, 95% CI for slope estimates of all covariates included zero.

Brood movements  $\geq 1$  km overland (i.e., without direct water links from the main lake to destination ponds) occurred in both years. Mean distance moved from nest locations during the first week was similar between years (2000:  $\bar{x}$  = 2.0 km, range: 0.1–4.2 km,  $n$  = 9 broods; 2001:  $\bar{x}$  = 2.3 km, range: 0.7–4.6 km,  $n$  = 6 broods). Model-averaged estimates from multistratum models lacked precision but suggested higher survival for broods that moved to habitats away from Karrak Lake (0.81; 95% CI: 0.60 to 1.02) than for those that remained on Karrak Lake (0.09; 95% CI: –1.70 to 1.88;  $n$  = 26 broods). However, most brood loss (96%; 22 of 23 broods) occurred on Karrak Lake, contributing to high variability in survival estimates on lake habitats. All marked broods that nested on Adventure Lake moved to Karrak Lake ( $n$  = 7) or other habitats ( $n$  = 2) within two days of hatch; no broods, marked or unmarked, were detected using Adventure Lake thereafter. Despite apparent higher survival when using other habitats, most ducklings remained on Karrak Lake ( $\hat{\psi}_{\text{Karrak-Other}}$  = 0.05, 95% CI: –0.04 to 0.13), and those that moved from Karrak Lake ( $n$  = 4 broods each in 2000 and 2001)



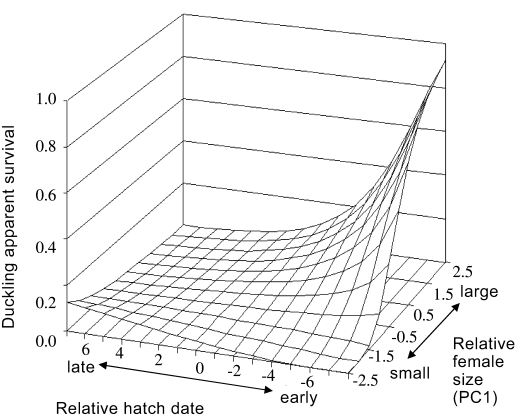


FIG. 3. Influence of female size and hatch date on duckling daily apparent survival as predicted by models for ducklings that remained with radiomarked females for the first 24 days after hatch at Karrak Lake, Nunavut, during 2001 and 2002. The relationship is based on weighted model averages and expresses the interaction between female size and hatch date, additive among age categories. Data are backtransformed from a logit scale ( $\hat{\beta}_{\text{female size}_{\text{in}}} = 0.54$ , 95% CI: 0.19 to 0.90;  $\hat{\beta}_{\text{hatch date}_{\text{in}}} = -0.33$ , 95% CI: -0.65 to 0.00;  $\hat{\beta}_{\text{female size}_{\text{in}} * \text{hatch date}_{\text{in}}} = -0.48$ , 95% CI: -0.03 to -0.92).

tended to remain on small ponds more often than they returned to Karrak Lake ( $\hat{\psi}_{\text{Other-Karrak}} = 0.04$ ; 95% CI: -0.01 to 0.09). Movement to other habitats generally occurred during the early part of brood-rearing. Nest failure and brood loss induced early departure of females (Table 4).

DISCUSSION

Our estimates of duckling survival, the first for King Eiders, were similar to survival rates reported for the closely related Common Eider (*S. mollissima*; 17-year  $\bar{x} = 10\%$ , Mendenhall and

Milne 1985; 1-year estimate = 19%, Flint et al. 1998). Most duckling mortality in King Eiders occurred shortly after hatch and was largely the result of total brood loss, which is common in most waterfowl (Orthmeyer and Ball 1990, Mauser et al. 1994). King Eider ducklings inhabit tundra lakes with no emergent aquatic vegetation; therefore, they can escape from predators only by diving or through maternal defense. Duckling motor skills are least developed shortly after hatch (Anderson 2000), rendering the youngest ducklings most vulnerable to predation (Mendenhall and Milne 1985). As in most other studies of duckling survival (Orthmeyer and Ball 1990, Mauser et al. 1994), we found that most mortality occurred early during the brood-rearing period (within two days of hatch). Predation by Glaucous Gulls (*L. hyperboreus*) and Herring Gulls (*L. argentatus*) was the sole observed cause of mortality for ducklings, as was found for Common Eiders (Mawhinney and Diamond 1999). We observed no mortality for ducklings 14 to 24 days old. This may be because, unlike most waterfowl (Gollop and Marshall 1954), King Eiders show extremely rapid growth for their body size and attain flight by 40 days of age (Parmelee et al. 1967); ducklings closely resembled adults in size by 24 days of age and no longer dived to elude predatory gulls.

Ducklings brooded by larger females survived at a higher rate than ducklings brooded by smaller females. We suggest that this may be the result of multiple factors, including (1) more efficient use of reserves (Kendeigh 1970, Calder 1974) that may enable larger conspecific females to spend less time foraging (see Goudie and Ankney [1986] for interspecific comparisons) and more time on alert for gulls; (2) increased maneuverability and physical strength, which may offer greater protection from gulls; (3) benefits of shared environments if King Eiders

TABLE 4. Number of days after hatch or nest failure that radiomarked female King Eiders on our study area surrounding Karrak Lake, Nunavut, were resighted during 2000 and 2001.

Status	2000			2001		
	Days ( $\bar{x}$ )	Birds ( <i>n</i> )	95% CI	Days ( $\bar{x}$ )	Birds ( <i>n</i> )	95% CI
Brooding females	25	9	22–26	22	4	15–27
Females with total brood loss	16	14	14–17	17	8	15–20
Failed nesters	10	7	5–14	15	17	12–17

exhibit natal philopatry to brood-rearing sites and if use of the same nutrient-rich brood-rearing areas during the early stages of life by both mothers and offspring improve growth and survival of each (Sedinger et al. 1995, Cox et al. 1998); or (4) the tendency for larger females to be more experienced breeders. Previous breeding experience can increase breeding success (Aldrich and Raveling 1983), and breeding propensity in King Eiders was related to size (Mehl 2004). However, maternal size advantages may be reduced if nesting is delayed (Fig. 3). Advantages of large female size for defense against gull predation appeared to be greatest early in the season, when attacks by gulls were likely fewest (Bédard and Munro 1976).

Brood amalgamation among King Eiders was relatively uncommon compared with that observed in Common Eiders (Bédard and Munro 1976) and White-winged Scoters (*Melanitta fusca deglandi*; Brown and Brown 1981, Traylor 2003). Presence of ducklings in foster broods concurrent with continuing care of siblings by natal females suggests accidental brood mixing. Although the significance of amalgamations remains unclear, our data did not provide evidence that King Eiders abandon their young entirely to the care of others. Rather, limited evidence for temporary abandonment suggests that at least some King Eider females may leave their broods for short periods of foraging or in search of better brood-rearing areas (see Afton and Paulus 1992). During periods of temporary abandonment, ducklings may join with other broods that share the same habitat. If female offspring-recognition is not developed, brood mixing may lead to accidental fostering; evidence for this includes observations of one female caring for the correct number of ducklings, only one of which was its own. Total brood loss by a natal female, in the presence of marked ducklings that had joined other broods, may give the false impression of abandonment. Importantly, given that ducklings from radio-marked females may have survived in other, nonmarked broods, our estimates of survival presented here likely represent minimum values of duckling and brood survival.

King Eider broods remained on freshwater habitats throughout the first 24 days of the brood-rearing period, despite movements by coastal-nesting conspecifics toward marine habitats after hatch (at sea ~15 days after hatch; Parmelee et al.

1967). Residents on local freshwater ponds may realize benefits from familiarity with local predators and safe roosting sites (Greenwood 1980). We did not continue observations until fledging, so females and broods may have used rivers to reach marine habitats after our observations ceased. Females without young left breeding areas earlier than those with young, which suggests that unsuccessful females may have moved to marine habitats (~60 km) to molt (Suydam 2000). By contrast, we observed brood females molting on freshwater habitats.

Brood movements away from the main nesting lakes resulted in increased duckling survival, because smaller freshwater ponds (1) provided improved foraging (see Cox et al. 1998), (2) had lower densities of foraging gulls than Karrak Lake or Adventure Lake, or (3) provided sheltered areas from the wind (winds on larger lakes may separate broods and aid in gull attacks; see Gilchrist et al. 1998). With such disadvantages in remaining on large lakes, we wonder why more broods did not disperse to ponds. However, most overland movements to ponds occurred soon after hatch, when duckling motor skills were least developed, so overland movement may have led to an undetected increase in mortality (Ball et al. 1975). Nevertheless, once broods reached ponds, they appeared to survive at a greater rate than on either Karrak Lake or Adventure Lake.

In conclusion, maternal body size in King Eiders can have an important influence on duckling survival. Use of individually marked ducklings and nesting hens and of models that account for detection probability provided a useful approach to estimation of survival while accounting for brood abandonment. Furthermore, use of radiotelemetry allowed continued detection of ducklings that had dispersed to smaller ponds away from the primary nesting by King Eiders. Otherwise, our estimates of true duckling survival would have been seriously biased low had our attention remained focused solely on the large lakes from which ducklings hatched. Without complete ability to detect live ducklings that had dispersed from Karrak Lake and Adventure Lake, disappearance of ducklings from the study area owing to brood dispersal would have been considered mortality. Research that combines these approaches is needed to provide unbiased estimates from which proper inferences about

variation in offspring survival can be drawn. Future studies that incorporate cross-fostering experiments would help distinguish maternal effects on covariates that appear to influence survival in King Eider ducklings.

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#### 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. 1985. Prediction and entropy. Pages 1–24 in *A Celebration of Statistics: The ISI Centenary Volume* (A. C. Atkinson and S. E. Fienberg, Eds.). Springer-Verlag, New York.
- ALDRICH, T. W., AND D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. *Auk* 100:670–679.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1990. Body size and fecundity in Lesser Snow Geese. *Auk* 107:440–443.
- ANDERSON, V. 2000. Egg size, duckling composition, growth and motor performance in King Eiders *Somateria spectabilis*. M.Sc. thesis, University of Saskatchewan, Saskatoon.
- BALL, I. J., D. S. GILMER, L. M. COWARDIN, AND J. H. RIECHMAN. 1975. Survival of Wood Duck and Mallard broods in north-central Minnesota. *Journal of Wildlife Management* 39:776–780.
- BÉDARD, J., AND J. MUNRO. 1976. Brood and crèche stability in the Common Eider of the St. Lawrence Estuary. *Behaviour* 60: 221–236.
- BLUMS, P., A. MEDNIS, AND J. D. NICHOLS. 1994. Retention of web tags and plasticine-filled leg bands applied to day-old ducklings. *Journal of Wildlife Management* 58:76–81.
- BROWN, P. W., AND M. A. BROWN. 1981. Nesting biology of the White-winged Scoter. *Journal of Wildlife Management* 45:38–45.
- BROWNIE, C., J. E. HINES, J. D. NICHOLS, K. H. POLLOCK, AND J. B. HESTBECK. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- CALDER, W. A., III. 1974. Consequences of body size for avian energetics. Pages 86–144 in *Avian Energetics* (R. A. Paynter, Jr., Ed.). Publications of the Nuttall Ornithological Club, no. 15.
- CHRISTENSEN, T. K. 1999. Effects of cohort and individual variation in duckling body condition on survival and recruitment in the Common Eider *Somateria mollissima*. *Journal of Avian Biology* 30:302–308.
- COOCH, E., R. F. ROCKWELL, AND S. BRAULT. 2001. Retrospective analysis of demographic responses to environmental change: A Lesser Snow Goose example. *Ecological Monographs* 71:377–400.
- COOKE, F., AND C. S. FINDLAY. 1982. Polygenic variation and stabilizing selection in a wild population of Lesser Snow Geese (*Anser caerulescens caerulescens*). *American Naturalist* 120:543–547.
- COULSON, J. C. 1984. The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *Ibis* 126:525–543.
- COX, R. R., JR., M. A. HANSON, C. C. ROY, N. H. EULISS, JR., D. H. JOHNSON, AND M. G. BUTLER.

1998. Mallard duckling growth and survival in relation to aquatic invertebrates. *Journal of Wildlife Management* 62:124–133.
- DZUBIN, A., AND E. G. COOCH. 1993. Measurements of Geese: General Field Methods. California Waterfowl Association, Sacramento.
- DZUS, E. H., AND R. G. CLARK. 1997. Brood size manipulation in mallard ducks: Effects on duckling survival and brooding efficiency. *Écoscience* 4:437–445.
- FLINT, P. L., C. L. MORAN, AND J. L. SCHAMBER. 1998. Survival of Common Eider *Somateria mollissima* adult females and ducklings during brood rearing. *Wildfowl* 49:103–109.
- FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- GILCHRIST, H. G., A. J. GASTON, AND J. N. M. SMITH. 1998. Wind and prey nest sites as foraging constraints on an avian predator, the Glaucous Gull. *Ecology* 79:2403–2414.
- GOLLOP, J. B., AND W. H. MARSHALL. 1954. A Guide for Aging Duck Broods in the Field. Mississippi Flyway Council Technical Section, Northern Prairie Wildlife Research Center, Jamestown, North Dakota.
- GOUDIE, R. I., AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475–1482.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- 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.
- KELLETT, D. K., AND R. T. ALISAUSKAS. 1997. Breeding biology of King Eiders nesting on Karrak Lake, Northwest Territories. *Arctic* 50:47–54.
- KELLETT, D. K., AND R. T. ALISAUSKAS. 2000. Body-mass dynamics of King Eiders during incubation. *Auk* 117:812–817.
- KENDEIGH, S. C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72:60–65.
- KORSCHGEN, C. E., K. P. KENOW, W. L. GREEN, D. H. JOHNSON, M. D. SAMUEL, AND L. SILEO. 1996. Survival of radiomarked Canvasback ducklings in northwestern Minnesota. *Journal of Wildlife Management* 60:120–132.
- LAMOTHE, P. 1973. Biology of the King Eider (*Somateria spectabilis*) in a fresh water breeding area on Bathurst Island, N.W.T. M.Sc. thesis, University of Alberta, Edmonton.
- LEBRETON, J.-D., T. ALMERAS, AND R. PRADEL. 1999. Competing events, mixtures of information and multistratum recapture models. *Bird Study* 46 (Supplement):39–46.
- MACHIN, K. L., AND N. A. CAULKETT. 2000. Evaluation of isoflurane and propofol anesthesia for intraabdominal transmitter placement in nesting female Canvasback ducks. *Journal of Wildlife Diseases* 36:324–334.
- MAUSER, D. M., AND R. L. JARVIS. 1991. Attaching radio transmitters to 1-day-old Mallard ducklings. *Journal of Wildlife Management* 55:488–491.
- MAUSER, D. M., R. L. JARVIS, AND D. S. GILMER. 1994. Survival of radio-marked Mallard ducklings in northeastern California. *Journal of Wildlife Management* 58:82–87.
- MAWHINNEY, K., AND A. W. DIAMOND. 1999. Using radio-transmitters to improve estimates of gull predation on Common Eider ducklings. *Condor* 101:824–831.
- MEHL, K. R. 2004. Brood ecology and population dynamics of King Eiders. Ph.D. dissertation, University of Saskatchewan, Saskatoon.
- MENDENHALL, V. M. 1979. Brooding of young ducklings by female eiders *Somateria mollissima*. *Ornis Scandinavia* 10:94–99.
- MENDENHALL, V. M., AND H. MILNE. 1985. Factors affecting duckling survival of eiders *Somateria mollissima* in northeast Scotland. *Ibis* 127:148–158.
- NICHOLS, J. D., J. E. HINES, K. H. POLLOCK, R. L. HINZ, AND W. A. LINK. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology* 75:2052–2065.
- ORTHEMEYER, D. L., AND I. J. BALL. 1990. Survival of Mallard broods on Benton Lake National Wildlife Refuge in north central Montana. *Journal of Wildlife Management* 54:62–66.
- PARMELEE, D. F., H. A. STEPHENS, AND R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. *National Museum of Canada Bulletin* 222.

- PELAYO, J. T. 2001. Correlates and consequences of egg size variation in wild Ruddy Ducks (*Oxyura jamaicensis*). M.S. thesis, University of Saskatchewan, Saskatoon.
- PRADEL, R., C. M. A. WINTREBERT, AND O. GIMENEZ. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics* 59: 43–53.
- ROCKWELL, R. F., E. G. COOCH, AND S. BRAULT. 1997. Dynamics of the mid-continent population of Lesser Snow Geese—Projected impacts of reduction in survival and fertility on population growth rates. Pages 73–100 in *Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group* (B. D. J. Batt, Ed.). Canadian Wildlife Service, Ottawa, Ontario, and U.S. Fish and Wildlife Service, Washington, D.C.
- SAS INSTITUTE. 1996. SAS/STAT User's Guide, version 6, 4th ed. SAS Institute, Cary, North Carolina.
- SEDINGER, J. S. 1992. Ecology of prefledgling waterfowl. Pages 109–127 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.
- SEDINGER, J. S., P. L. FLINT, AND M. S. LINDBERG. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology* 76:2404–2414.
- SUYDAM, R. S. 2000. King Eider. In *The Birds of North America*, no. 491 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- TRAYLOR, J. J. 2003. Nesting and duckling ecology of White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan. M.Sc. thesis, University of Saskatchewan, Saskatoon.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111–113.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–138.

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