

Factors Influencing Nesting Success of King Eiders on Northern Alaska's Coastal Plain

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ABSTRACT King eider (*Somateria spectabilis*) populations have declined markedly in recent decades for unknown reasons. Nest survival is one component of recruitment, and a female's chance of reproductive success increases with her ability to choose an appropriate nesting strategy. We estimated variation in daily nest survival of king eiders at 2 sites, Teshekpuk and Kuparuk, Alaska, USA, 2002–2005. We evaluated both a priori and exploratory competing models of nest survival that considered importance of nest concealment, seclusion, and incubation constancy as strategies to avoid 2 primary egg predators, avian (*Larus* spp., *Stercorarius* spp., and *Corvus corax*) and fox (*Alopex lagopus*). We used generalized nonlinear techniques to examine factors affecting nest survival rates and information-theoretic approaches to select among competing models. Estimated nest survival, accounting for a nest visitation effect, varied considerably across sites and years (0.21–0.57); however, given our small sample size, much of this variation may be attributable to sampling variation ($\sigma^2_{\text{process}} = 0.007$, 95% CI: 0.003–0.070). Nest survival was higher at Kuparuk than Teshekpuk in all years; however, due to the correlative nature of our data, we cannot determine the underlying causes with any certainty. We found mixed support for the concealed breeding strategy; females derived no benefit from nesting in areas with more willow (*Salix* spp.; measure of concealment) except that the observer effect diminished as willow cover increased. We suggest these patterns are due to conflicting predation pressures. Nest survival was not higher on islands (measure of seclusion) or with increased incubation constancy but was higher post-fox removal, indicating that predator control on breeding grounds could be a viable management option. Nest survival was negatively affected by our nest visitations, most likely by exposing the nest to avian scavengers. We recommend precautions be taken to limit the effects of nest visits in future studies and to consider them as a possible negative bias in estimated nest survival. Future models of the impacts of development within the breeding grounds of king eider should consider the influence of humans in the vicinity of nests. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1781–1789; 2008)

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The western North American population of king eiders (*Somateria spectabilis*) has declined by >50% between 1976 and 1996 for unknown reasons (Suydam et al. 2000). Eiders generally experience low and variable nest survival, one component of population recruitment (Lamothe 1973, Goudie et al. 2000, Petersen et al. 2000, Kellett et al. 2003). Reproductive success of a female depends, in part, upon successfully incubating a clutch and surviving to nest again. Any adaptations that serve to increase nest success, even slightly, may have a high selective value (Ricklefs 1984), although trade-offs between life-history traits could influence selection. Although population growth rate is often considered to have a low sensitivity or elasticity with respect to nest success, high inherent variation in nesting success can influence population dynamics (Hoekman et al. 2002, Flint et al. 2006). Predators are probably the most important selective force affecting nest success in birds (Ricklefs 1969, Martin 1995), resulting in a variety of strategies related to nest protection, including breeding synchrony, coloniality, distraction behavior, concealment, incubation behavior, and aggressive nest defense. However, options for avoiding predation are constrained by available habitat and condition of the female.

Larson (1960) argued that 2 main evolutionary strategies are used by Arctic tundra-nesting birds that have a limited ability to defend their nests: secluded nesting (success is

increased through greater inaccessibility of nest location) or concealed nesting (success is increased through more concealed nest location on the open tundra of the mainland and appropriate behavior). In most waterfowl, and eiders in particular, the main option for secluded breeding is to nest on islands. However, this strategy does not provide any protection from avian predators, such as gulls (*Larus* spp.) and jaegers (*Stercorarius* spp.). Concealed breeders may have some degree of protection from both avian and mammalian egg predators. The concealed breeding strategy relies on the nest and hen being camouflaged to some degree, usually by the vegetation around the nest. Hens also use behavioral strategies for concealment, including spacing of nests and choices in number and length of recesses she takes during incubation. Although king eiders typically cover their eggs when they take a recess (Parmelee et al. 1967, Lamothe 1973), the activity of moving to and from the nest may attract predators, and while on recess the female is unable to defend the nest.

Predators of king eider eggs fall into 2 categories, avian (gulls, jaegers, and ravens [*Corvus corax*]) and mammalian (arctic fox [*Alopex lagopus*]; Lamothe 1973, Kellett 1999), and strategies to avoid predation likely vary between the two. Larson (1960) argued that king eiders have an inferior to medium adaptation to fox predation, suggesting that nest-site selection may have evolved in the absence of heavy fox predation. Incubating eiders are unable to defend their nests from foxes (Lamothe 1973; P. Flint, United States

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Geological Survey, unpublished data) and do not feign injury to draw potential predators from the nest (Larson 1960), potentially relying on strategies of seclusion (island nesting), solitary nesting, and concealment. King eiders have been known to successfully deter predation attempts by gulls (Kellest and Alisauskas 1997) and jaegers (Blomqvist and Elander 1988), and most avian depredation events occur during periods when the incubating female is absent from the nest (P. Flint, unpublished data) and maintaining high incubation constancy is thought to be a strategy aimed at avoiding avian depredation (Milne 1976, Swennen et al. 1993, Bolduc et al. 2005). Therefore, to avoid avian predation it would be advantageous to maintain high incubation constancy and nest in an area with more cover; nests with a high degree of cover should be less obvious both when attended and unattended.

Our goal was to evaluate factors influencing nest survival of king eiders on the coastal plain of northern Alaska, USA. We hypothesized that king eiders may be under competing selection pressures associated with 2 primary egg predators, avian and fox, and that nesting strategies could reflect this dual pressure. First, we predicted that nest survival would be higher on islands if king eiders benefit from seclusion from mammalian predators. Second, we predicted that nest survival is higher in areas with taller vegetation (concealment), as measured by percent willow (*Salix* spp.) near the nest, and at nests where the female maintains higher attendance rates so as to minimize avian egg depredation. We also examined other sources of variation in daily survival rates including both ecological (season date and nest age) and anthropogenic variables (observer effect) in our models.

STUDY AREA

We studied king eiders nesting at 2 sites on the North Slope of Alaska, one near Teshekpuk Lake (153°07'W, 70°25'N) and another within the Kuparuk oilfields (149°41'W, 70°27'N), from 2002 to 2005. The Teshekpuk study site was approximately 10 km inland from the southeast shore of Teshekpuk Lake and experienced minimal human impact (i.e., no roads, communities, or development for petroleum extraction). The Kuparuk study site was in an area between the Colville and Kuparuk river deltas, which was developed for petroleum production and had an associated road network and human activities. The study sites were characterized by numerous thaw lakes, ponds, and basins. Wetland community types included wet sedge (*Carex* spp.) meadows, moist sedge-dwarf shrub (e.g., willow) meadows, and emergent sedge and pendant grass (*Arctophila fulva*) on the margins of lakes and ponds (Anderson et al. 1999). Dwarf willow was the dominant shrub and the main source of cover for nesting waterfowl.

METHODS

We systematically searched wetland basins on foot for king eider nests, beginning in mid-June at both sites in all years (2002–2005). We searched a larger area at Kuparuk (Kuparuk approx. 1,500 ha; Teshekpuk approx. 1,000 ha)

because a road system facilitated access there. We marked nests with a tongue depressor placed 1 m from the nest in vegetation, so as to be concealed from potential nest predators, and recorded latitude and longitude of each nest using a handheld Global Positioning System unit. We calculated nest-initiation dates by either backdating from known laying dates or from estimating incubation stages by candling eggs (Weller 1956) and assuming a laying interval of one egg per day and an incubation length of 23 days (Lamothe 1973). We monitored all nests once per week. After the initial nest visit, we tried not to flush hens from their nests. We designated a successful hatch by presence of either eggshells with detached membranes (Girard 1939) or ducklings. If there were eggshells with no membranes, or if the entire clutch was absent, we considered the nest depredated.

We classified nest sites as island or mainland after most nests had hatched; we defined islands as sites where we had to cross any depth and distance of water to reach them. Water levels tended to drop during the season and some nest sites that were islands during initiation of nest building were mainland at hatch. However, this only affected very shallow-water islands where it was questionable if water level provided any protection at any point in the season. We recorded percent cover by willow within 1 m of the nest after hatch.

We placed data loggers (HOBO-TEMP; Onset Computer Corporation, Pocasset, MA) opportunistically in nests at Teshekpuk ($n = 36$) and Kuparuk ($n = 30$) and programmed them to record nest temperature every 2 minutes. We used blown chicken eggs, dyed olive green and attached to a bolt, to hold thermistor probes. We drove the bolt into the ground under the nest, anchoring the probe and dummy egg in the nest (see Quakenbush et al. 2004), which allowed for a quick response to any change in temperature because the probe had only an eggshell between it and the incubating female. We defined incubation constancy as the percentage of time the female was on her nest over the period of days for which we had data. All aspects of the field work were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (UAF IACUC 05-29-King Eider).

Data Analysis

Site characteristics.—We used general linear models to evaluate factors influencing percent willow within 1 m of the nest (willow) using 3 a priori candidate models with variables site and island or mainland location ($Willow_{site}$, $Willow_{island}$, $Willow_{island,site}$). Similarly, we evaluated factors influencing initiation of egg-laying using 3 a priori candidate models with variables site and year ($Initiation_{site}$, $Initiation_{year}$, $Initiation_{site,year}$). We selected the best approximating models using Akaike's Information Criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2002).

Modeling daily nest-survival rate.—We evaluated competing biologically relevant, models of daily survival rate (DSR) of nests using generalized nonlinear mixed models

(Rotella et al. 2004, Stephens et al. 2005). We used PROC NLMIXED in SAS as described by Rotella et al. (2004) because it allowed us to model our binomially distributed data and consider the effects of both time-varying and time-invariant covariates on nest survival (SAS Institute, Cary, NC). We modeled the relationships between DSR and covariates with a logit link function (see Stephens et al. 2005) and selected the best approximating models using AIC_c (Burnham and Anderson 2002). We present the odds ratios and their 95% confidence intervals as a measure of the effect size of the variables in our models. Odds ratios = 1.0 imply no survival differences, and therefore odds ratio confidence intervals that include 1.0 indicate that the covariate does not significantly affect survival. For example, an odds ratio of 0.80 for the comparison of nest survival on islands versus mainland indicates that the odds of nest survival on islands were 20% lower than nest survival on the mainland (Corcoran et al. 2007).

We back-transformed logit-scale regression equations to get real DSR estimates, and we obtained period-specific survival as the product of the age-specific DSR estimates. We used a period length of 27 days: 23 days of incubation (Lamothe 1973) and 4 days of laying (average 4-egg clutch; one egg laid/day). We approximated variance of overall nest survival using bootstrapping simulation (Efron and Tibshirani 1993). We produced 1,000 bootstrapped resamples of the original data set (i.e., resampling nests with replacement, up to the original sample size within each site-year; PROC SURVEYSELECT) and estimated nest survival for each using the best approximating model. We used the standard deviation among the 1,000 bootstrapped estimates (for each site-yr) as the standard error for overall nest survival in each site-year (Efron and Tibshirani 1993). We estimated spatiotemporal process variation in nest survival using variance-components approaches outlined by Burnham et al. (1987). We used the variance among the 1,000 bootstrapped nest survival estimates as our estimate of sampling variance within a given site-year.

We model-averaged parameter estimates (θ) and associated variances from the candidate model set (Burnham and Anderson 2002). Additionally, we reported odds ratios of the model-averaged parameter estimates and their 95% confidence intervals. We calculated relative importance of each predictor variable as the sum of Akaike weights across all models in the set where the variable occurred (Burnham and Anderson 2002). We report values as mean \pm standard error.

Model justification and prediction.—We investigated 3 candidate model sets: the first to investigate ecological factors influencing nest survival of king eiders on the coastal plain of northern Alaska; the second to estimate nest survival, sampling error, and process error; and the third to investigate the effect of incubation constancy on nest survival using a subset of the data. We used a multiple model set approach so that we could investigate ecological questions using a complex set of models that could potentially make nest-survival estimation difficult or im-

possible (e.g., Dinsmore et al. 2002). Further, separate nest-survival estimates for sites and years are important for future population modeling and may not be a product of the top model from the ecological factors model set.

The first model set included 15 a priori models that examined effects of year, site, daily nest age, a time trend, observer effects, and 2 covariates: island or mainland nest location (island), and percent willow within 1 m of the nest (willow). Our simplest model was that of constant daily survival (model 1); we then modeled the main effects of site (model 2) and year (model 3) separately. The DSR may vary across the nesting season (time trend) if external factors such as weather or available forage vary predictably across the season. The DSR may also increase with age of the nest (age) as the reproductive value of the attempt increases, or due to nests with inherently lower survival probabilities being less likely to persist in the sample as incubation progresses. Therefore, for each of these 2 main-effects models, we fit 3 additional additive models, one with a linear trend through time within the season on daily nest survival (models 4 and 7), one with nest age effects (models 5 and 8), and a third with both (models 6 and 9). The DSR may be higher on islands because females may derive some protection from mammalian egg predators there (secluded strategy) or higher at nests with more cover (concealed strategy). We modeled effects of 2 covariates (island and willow) by adding each one separately (models 10 and 12) to the best model (DSR_{site}) from the set of 9 models that we had run thus far and then included an interaction with the main effect in the model (models 11 and 13). Our small data set limited the number of models we could investigate (Burnham and Anderson 2002), so we added these covariates in a hierarchical manner (Langtimm et al. 1998, Stephens et al. 2005). Additionally, we included an interaction with site, year, and island in one model because there was fox control in 2005 at the Kuparuk study area, which could have influenced the effect of islands in that year (model 14).

Researchers typically visit nests periodically to determine nest success, sometimes displacing birds off their nests in the process (Mayfield 1975). Disturbance associated with regular nest visits may affect success of those nests under observation (i.e., observer effect; Bart 1977, Mayer-Gross et al. 1977, Bart and Robson 1982, Rotella et al. 2000, Lloyd and Plagány 2002). Observer effect may be caused by exposing the nest to predation following displacement of the parents or by attracting or repelling predators (reviewed by Götmark 1992). Because small changes in DSR translate into large changes in nest success, small observer effects can strongly affect estimates of nesting success and may even yield misleading conclusions regarding population viability (Rotella et al. 2000). Specifically, we created an index variable that took the value of one on the first day of the interval after the nest was visited and zero otherwise (Rotella et al. 2000). We then used this variable to evaluate whether there was an effect on daily survival rates the day following a nest visit by adding it to the best model (DSR_{site} ; model 15).

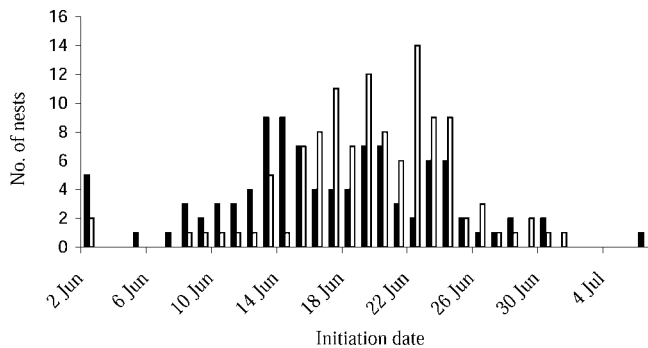


Figure 1. Distributions of nest initiation dates for king eiders nesting at Teshekpuk (white bars) and Kuparuk (black bars), Alaska, USA, 2003–2005.

After the initial a priori model selection process, we built 2 exploratory models with an interaction between observer effect in the best model and island ($DSR_{site,observer,island,observer \times island}$), and willow ($DSR_{site,observer,willow,observer \times willow}$), and a third that considered effects of both island and willow ($DSR_{site,island,willow}$).

The second a priori candidate model set considered each site year separately and included models with additive and multiplicative effects of initiation of laying (init) and nest age (age) on daily nest survival. As observer effects were important in the first model set, we built an exploratory model that included an additive observer effect to the top a priori model. We used the top models before and after the inclusion of the exploratory model to estimate daily nest survival, period-specific survival, sampling variances, and process error among site years. We estimated observer-related reductions to nest survival by calculating nest survival from both DSR models in which observer effects were accounted for (via model structure) but not included in back-transformation calculations, and nest survival from models in which observer effects were unseparated from natural mortality (i.e., no observer effect term in the model; Wilson 2007).

The third a priori candidate model set considered a subset of the data to evaluate the effect of incubation constancy on daily nest survival. We did not have estimates of incubation constancy for all nests in the first model set, forcing us to employ this additional exercise in model selection. This model set included the top model from the first model set, constant daily survival, and an additive effect of incubation constancy on both previous models.

RESULTS

We monitored 289 king eider nests over 4 years. Annual number of nests ranged from 30 to 42 at Kuparuk and from 33 to 42 at Teshekpuk. Initiation of egg laying varied between sites; the top model of the candidate model set ($Initiation_{site}$; $AIC_c = 692.76$, AIC_c wt = 0.80) was 3.39 AIC_c units from the next best model ($Initiation_{site,year}$). Parameter estimates (effect sizes, θ) from the top model indicated that initiation was later at Teshekpuk than Kuparuk ($\theta_{site} = -1.48$, 95% CI = -2.91 to -0.05). On

average, females at Kuparuk initiated egg laying on 17 June and at Teshekpuk on 19 June. First nests were initiated the first week in June each year and egg laying continued through the end of June (Fig. 1). We observed arctic fox, glaucous gulls (*L. hyperboreus*), and parasitic (*Stercorarius parasiticus*) and long-tailed (*Stercorarius longicaudus*) jaegers depredating nests. Ravens and red fox (*Vulpes vulpes*) were also present in the study areas.

The top model of the candidate model set describing percent willow within 1 m of the nest ($Willow_{site,island}$; $AIC_c = -1,001.27$) was 2.84 AIC_c units from the next best model ($Willow_{site}$) and carried 81% of the AIC_c weight. Percent willow ranged from 0% to 95% and differed between sites ($\theta_{site} = -0.09$, 95% CI = -0.13 to -0.05); Teshekpuk had on average double the amount of willow ($18.1 \pm 2.3\%$) than did Kuparuk ($9.0 \pm 0.8\%$). Overall, most (95%) nests had <50% cover by willow, and nests on islands had more willow ($\theta_{island} = -0.05$, 95% CI = -0.09 to -0.01) than did mainland nests. Proportions of nests on islands were similar between the 2 sites (Kuparuk: 50%; Teshekpuk: 55%).

The best approximating a priori model describing ecological factors influencing king eider nest success included effects of site and observer ($DSR_{site,observer}$) and was 3.37 AIC_c units from the next best model (DSR_{site}). All models within 7 AIC_c units of the top model included effects of site (Table 1). The best approximating model indicated that the odds of nest survival were 40% lower at Teshekpuk than Kuparuk ($\beta_{site} = -0.5$, 95% CI = -0.8 to -0.2 ; odds ratio = 0.6, 95% CI = 0.4–0.8) and 60% higher on days when nests were not revisited ($\beta_{observer} = -0.9$, 95% CI = -1.7 to -0.2 ; odds ratio = 0.4, 95% CI = 0.2–0.9).

Including the 3 exploratory models changed the ranking of the top models. The exploratory model $DSR_{site,observer,observer \times willow}$ was the top ranked model when included and was 5.17 AIC_c units from the next best model ($DSR_{site,observer}$), the top a priori model. The exploratory models $DSR_{site,observer,island,observer \times island}$ and $DSR_{site,island,willow}$ were 8.04 and 11.13 AIC_c units from the top model ($DSR_{site,observer,willow,observer \times willow}$), respectively. The best approximating exploratory model indicated that DSR was higher at Kuparuk than Teshekpuk ($\beta_{site} = -0.5$, 95% CI = -0.8 to -0.1 ; odds ratio = 0.6, 95% CI = 0.4–0.9) and that there was an effect of willow cover in concert with an observer effect. Nest survival was lower at nests with a higher percentage of cover from willow on days when nests were not revisited ($\beta_{willow} = -1.8$, 95% CI = -0.5 to -3.1 ; odds ratio = 0.2, 95% CI = 0.1–0.6), but higher on days when the nest was visited ($\beta_{observer \times willow} = 6.1$, 95% CI = 2.3–10.0; odds ratio = 465.4, 95% CI = 9.8–22,057.3; Fig. 2), although this effect size was poorly estimated. Model-averaged odds ratios indicated that nest survival decreased as willow cover increased and was higher at Kuparuk and on days when the nest was not visited (Table 2). There was little support for the parameters island, nest age, and time trend, and model-averaged odds ratios indicated no effect (Table 2). The exploratory model including an interaction between observer and island had little support, and the

Table 1. A priori models of daily survival rate (DSR) of king eider nests found at Teshekpuk and Kuparuk, Alaska, USA, 2002–2005. Factors in models included year, site, island or mainland nest location (island), logit-linear trends with time (time trend), daily nest age (age), percentage of willow within 1 m of nest bowl (willow), and an observer effect.

| DSR model | K^a | AIC_c^b | ΔAIC_c^c | w_i^d | Deviance |
|--|-------|-----------|------------------|---------|----------|
| Site, observer | 3 | 801.65 | 0 | 0.54 | 795.64 |
| Site | 2 | 805.02 | 3.37 | 0.1 | 801.02 |
| Site, age | 3 | 805.66 | 4.01 | 0.07 | 799.65 |
| Site, island | 3 | 805.89 | 4.23 | 0.07 | 799.88 |
| Site, time trend | 3 | 806.04 | 4.38 | 0.06 | 800.03 |
| Site, willow | 3 | 806.89 | 5.24 | 0.04 | 800.88 |
| Site, time trend, age | 4 | 807.66 | 6.01 | 0.03 | 799.64 |
| Site, island, site \times island | 4 | 807.73 | 6.07 | 0.03 | 799.71 |
| Site, island, yr, site \times island, yr \times island | 10 | 807.95 | 6.3 | 0.02 | 787.87 |
| Site, willow, site \times willow | 4 | 808.44 | 6.79 | 0.02 | 800.43 |
| Yr | 4 | 810.96 | 9.31 | 0.01 | 802.94 |
| (.) | 1 | 811.04 | 9.39 | 0.01 | 809.04 |
| Yr, age | 5 | 811.21 | 9.55 | 0.01 | 801.18 |
| Yr, time trend | 5 | 811.24 | 9.59 | 0.01 | 801.22 |
| Yr, time trend, age | 6 | 813.04 | 11.39 | 0 | 801.01 |

^a No. of parameters in the model.

^b Akaike's Information Criterion adjusted for small sample size.

^c Difference between model AIC_c and AIC_c value of the best model.

^d AIC_c wt.

interaction was imprecisely estimated ($\beta_{\text{observer} \times \text{island}} = -0.2$, 95% CI = -1.7 to 1.3; odds ratio = 0.8, 95% CI = 0.2–3.6).

The top a priori model from the candidate model set for estimation of nest survival, $DSR_{\text{site, year, age, site} \times \text{year, site} \times \text{age, year} \times \text{age}}$, was 2.33 AIC_c units from the next best model (Table 3). Daily nest survival varied among site years and with age of the nest; however, all odds ratios 95% confidence intervals overlapped 1, indicating no effect. The exploratory model $DSR_{\text{site, year, age, site} \times \text{year, site} \times \text{age, year} \times \text{age, observer}}$ ($AIC_c = 799.76$, AIC_c weight = 0.79) was an improvement of 3.85 AIC_c units on the top a priori model. Daily nest survival was lower when visited by an observer ($\beta_{\text{observer}} = -1.03$, 95% CI = -1.91 to -0.16; odds ratio = 0.36, 95% CI = 0.15–0.85), as we found in the first model set. Nest survival ranged from 0.12 to 0.26 at Teshekpuk and from 0.10 to 0.43 at Kuparuk when the observer effect was not accounted for (i.e., no observer effect term in model). Nest survival estimated from the model controlling for an observer effect via model structure was much higher, 0.22 to 0.40 at Teshekpuk and 0.21 to 0.57 at Kuparuk (Table 4). Estimated site-year-specific process variation in DSR was 0.010 (95% CI = 0.007–0.075; $DSR_{\text{site, year, age, site} \times \text{year, site} \times \text{age, year} \times \text{age}}$). Estimated site-year-specific process variation using the exploratory model $DSR_{\text{site, year, age, site} \times \text{year, site} \times \text{age, year} \times \text{age, observer}}$ was 0.007 (95% CI = 0.003–0.070).

We did not find an effect of incubation constancy on nest survival. Addition of the constancy variable added 2 AIC_c units but did not change deviance (Table 5). Odds of nest survival increased 2.1-fold for each unit increase in constancy; however, the estimated effect was imprecise ($\beta_{\text{constancy}} = 0.73$, 95% CI = -7.9 to 9.4; odds ratio = 2.1, 95% CI = -0.00 to 11,118.5).

DISCUSSION

King eiders breeding on the coastal plain of northern Alaska over the 4 years of our study experienced somewhat higher

nest success (21–57%) than reported for king eiders nesting in the High Arctic (0–21%; Lamothe 1973). However, semicolonial, island-nesting king eiders in Nunavut, Canada, had higher nest success (30–89%; Kellett et al. 2003), presumably due to the benefits of nesting on isolated islands. Our estimates were within the range reported for common (*Somateria mollissima*; Spitzbergen 27–93%, Ahlén and Andersson 1970; Beaufort Sea, AK 33%, Schamel 1977) and spectacled eiders (*Somateria fischeri*; western AK 18–76%, Grand and Flint 1997; Arctic Russia 2–30%, Pearce et al. 1998). Nest survival for king eiders was highly variable on both temporal and spatial scales on the coastal plain of northern Alaska. However, process variance was low, indicating that most variance was from sampling, potentially due to our small sample size.

We found mixed support for the concealed breeding strategy, possibly due to king eiders being caught between competing selection pressures associated with avian and mammalian egg predation. To avoid avian predation it should be advantageous to nest in areas with willow cover

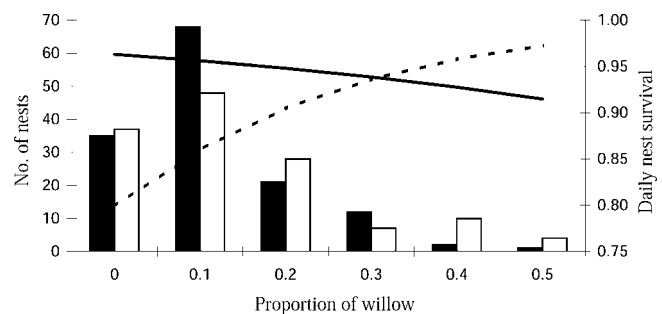


Figure 2. Predicted daily survival rates of king eider nests at Teshekpuk, Alaska, USA, 2002–2005, on the day when an observer visits (dashed line) and does not visit (solid line) in relation to the proportion of willow within 1 m of the nest site. Frequency of nests at Teshekpuk (white bars) and Kuparuk (black bars), Alaska, in relation to proportion of willow within 1 m of the nest site.

Table 2. Model-averaged parameters ($\hat{\theta}$), odds ratios, and associated 95% confidence intervals for explanatory variables from the set of a priori and exploratory models of daily nest survival for female king eiders ($n = 289$) nesting at Teshekpuk and Kuparuk, Alaska, USA, 2002–2005.

| Variable | $\hat{\theta}$ | $\hat{\theta}$ 95% CI | Odds ratio | Odds ratio 95% CI | Relative importance ^a |
|-----------------|----------------|-----------------------|------------|-------------------|----------------------------------|
| Site | -0.476 | -0.808, -0.144 | 0.621 | 0.446, 0.866 | 0.997 |
| Observer | -1.694 | -2.591, -0.796 | 0.184 | 0.075, 0.451 | 0.942 |
| Willow | -1.534 | -2.677, -0.402 | 0.216 | 0.069, 0.669 | 0.872 |
| Island | 0.008 | -0.009, 0.026 | 1.008 | 0.991, 1.026 | 0.032 |
| Age | 0 | 0.000, 0.001 | 1 | 1.000, 1.001 | 0.013 |
| Time trend | 0 | 0.000, 0.000 | 1 | 1.000, 1.000 | 0.011 |
| Yr ^b | | | | | |
| 2003 | 0.001 | -0.002, 0.004 | 1.001 | 0.998, 1.004 | 0.006 |
| 2004 | -0.001 | -0.004, 0.002 | 0.999 | 0.996, 1.002 | 0.006 |
| 2005 | 0.002 | -0.001, 0.005 | 1.002 | 0.999, 1.005 | 0.006 |

^a Variables are not represented equally in the model set.

^b Parameter estimates for yr are relative to 2002.

because nests are less likely to be detected both when attended and unattended. Evidence for this benefit can be seen in the decreasing observer effect as willow cover increases. The primary source of nest loss associated with observer effects is likely avian predators taking advantage of exposed nests (Bolduc and Guillemette 2003). However, in the absence of observers, nest success was actually lower at nest sites with more cover from willow. This negative effect of cover may be a reflection of an unmodeled variable that was correlated with percent willow (e.g., distance to water) or to different predators being responsible for observer-induced mortality. Although foxes are unlikely to be actively searching for king eider nests because nests occur in such low densities in our study area, foxes may focus on foraging in areas with willow cover as the most efficient habitat for them to hunt, increasing their likelihood of approaching prey undetected or because prey densities are generally higher in these habitats. Thus, the overall negative association between nest survival and willow cover may actually be driven by fox predation. We argue that selection of willow cover is an adaptation to avoid avian predation and that nest habitat selection by king eider may have evolved in the absence of heavy fox predation, resulting in an ineffective strategy at current fox population levels. It is important to remember that we drew these conclusions from an exploratory model and they should be viewed with

caution; more research is needed to explore competing selection pressures associated with predation pressure.

King eiders did not have increased nest success on islands, contrary to our predictions regarding avoidance of mammalian predation. Our definition of islands included those in very shallow water, which is unlikely to offer much deterrent to mammalian predators and may have contributed the lack of finding an effect. Kellett et al. (2003) found that king eiders had greater nest success on more isolated islands (farther from the mainland) and their exclusively island-nesting population at Karrak Lake experienced much higher success (30–89%) than reported for mainland populations (0–56%; Lamothe 1973, this study). However, the islands at Karrak Lake were much larger and in deeper water, and likely provided more complete protection than the islands in shallow-water tundra ponds that characterize much of the king eiders' circumpolar breeding areas. Further, the Karrak Lake eiders are nesting within a large lesser snow (*Chen caerulescens*) and Ross' goose (*C. rossii*) colony, which could provide a buffer from predators. King eiders nesting in areas without deepwater islands may not have a viable option for secluded nesting. Low densities of both nesting king eiders and foxes may be required for successful breeding in absence of secluded nest sites.

It has been suggested that king eiders nest in association with jaegers (Lamothe 1973, Blomqvist and Elander 1988), gulls (Götmark and Åhlund 1988), and terns (*Sterna*

Table 3. Model selection results for estimation of nest survival of king eider nests found at Teshekpuk and Kuparuk, Alaska, USA, 2002–2005. Factors in models included year, site, daily nest age (age), and initiation date (init).

| DSR ^a model | K^b | AIC _c ^c | ΔAIC_c^d | w_i^e | Deviance |
|---|-------|-------------------------------|------------------|---------|----------|
| Site, yr, age, site \times yr, site \times age, yr \times age | 13 | 803.61 | 0 | 0.56 | 777.48 |
| Site, yr, init, age, site \times yr, site \times init, yr \times init, site \times age, yr \times age | 18 | 805.94 | 2.33 | 0.17 | 769.68 |
| Site, yr, site \times yr | 8 | 807.38 | 3.77 | 0.09 | 791.33 |
| Site, yr, init, site \times yr | 9 | 807.46 | 3.85 | 0.08 | 789.39 |
| Site, yr, age, site \times yr | 9 | 808.08 | 4.47 | 0.06 | 790.01 |
| Site, yr, init, site \times yr, site \times init, yr \times init | 13 | 809.43 | 5.81 | 0.03 | 783.29 |
| (.) | 1 | 811.04 | 7.43 | 0.01 | 809.04 |

^a Daily survival rate.

^b No. of parameters in the model.

^c Akaike's Information Criterion adjusted for small sample size.

^d Difference between model AIC_c and AIC_c value of the best model.

^e AIC_c wt.

Table 4. Estimates of nest survival and standard error from the top a priori and exploratory models of king eiders at Teshekpuk and Kuparuk, Alaska, USA, during 2002–2005. The top a priori model ($DSR_{site,year,age,site \times year,site \times age,year \times age}$) does not separate observer effects from natural mortality, whereas the top exploratory model ($DSR_{site,year,age,site \times year,site \times age,year \times age,observer}$) accounted for observer effects via model structure, but we did not include these effects in back-transformation calculations, effectively estimating nest survival as though the nests were never visited.

| Site | Yr | <i>n</i> ^a | No observer effect | | Controlled for observer effect | |
|-----------|------|-----------------------|--------------------|------|--------------------------------|------|
| | | | Nest survival | SE | Nest survival | SE |
| Teshekpuk | 2002 | 42 | 0.26 | 0.06 | 0.4 | 0.11 |
| | 2003 | 40 | 0.13 | 0.06 | 0.22 | 0.10 |
| | 2004 | 33 | 0.12 | 0.05 | 0.23 | 0.11 |
| | 2005 | 35 | 0.14 | 0.06 | 0.27 | 0.11 |
| Kuparuk | 2002 | 42 | 0.42 | 0.11 | 0.56 | 0.12 |
| | 2003 | 35 | 0.23 | 0.09 | 0.38 | 0.13 |
| | 2004 | 30 | 0.10 | 0.05 | 0.21 | 0.12 |
| | 2005 | 32 | 0.43 | 0.10 | 0.57 | 0.12 |

^a No. of nests in each site yr.

paradisaea; Kellett and Alisauskas 1997) to take advantage of the defensive behavior of these species toward shared nest predators. However, king eiders nesting at Kuparuk and Teshekpuk appeared to avoid nesting near gulls; the average distance to the closest glaucous gull nests was 0.5–1.0 km (R. L. Bentzen, University of Alaska Fairbanks, unpublished data), well beyond the reported range for receiving secondary protection (Schamel 1977, Götmark and Åhlund 1988). Further, glaucous gulls are unable to repel foxes from their territories (P. Flint, unpublished data), suggesting that only avian predation pressures would be alleviated through associations with gulls. Similarly, we found no evidence of cooperation with nesting conspecifics to take advantage of their defense behaviors; king eiders in our study sites were dispersed across the landscape, averaging 477 m (\pm 31.2 m) between nests.

Nest success was higher at Kuparuk than Teshekpuk, sites distant enough to be considered independent (approx. 160 km) and that differ in a variety of ways. For one, Kuparuk was within an area that has been developed for oil and gas extraction. Effects of development on animal populations include increased densities of predators in oilfields, mainly due to anthropogenic food sources (Eberhardt et al. 1982, Truett et al. 1997, Burgess 2000). These predators (foxes, gulls, jaegers, and ravens) prey on eggs, nestlings, and fledglings of many birds, including king eiders (Larson 1960, Lamothe 1973, Kellett and Alisauskas 1997). Increased predator populations may lead to decreased nest survival of tundra-nesting birds, unless predators are largely

subsidized by anthropogenic food sources. It seems counter-intuitive that higher nest survival at Kuparuk is a direct result of increased predator abundances. However, it is unknown whether predator densities do actually vary between Kuparuk and Teshekpuk and to what extent they are subsidized by anthropogenic food sources. The largest difference in nest success between the 2 sites was in the summer of 2005, prior to which 41 foxes were trapped and killed at Kuparuk (C. Rea, ConocoPhillips Inc., personal communication), potentially causing the very high nest success (56%) recorded that year. However, as nest success was consistently higher at Kuparuk in all years, we do not believe the 2005 predator removal alone caused site differences.

Habitat quality may vary between the 2 sites and drive differences in nest survival. Potential differences include degree of concealment available at potential nest sites, food availability, and other microhabitat variables. There is some indication that king eiders had higher food availability because their incubation breaks were shorter, yet birds lost mass at the same rate at Kuparuk (Bentzen et al., in press). The resulting increased incubation constancy at Kuparuk may have led to increased nest success if most egg depredation occurred during incubation recesses. However, we found no relationship between incubation constancy and nest survival on the individual level, possibly due to the lack of variation in incubation constancy (making it difficult to detect an effect) or sample size or because there is no current benefit to higher versus lower incubation constancy within

Table 5. Model selection results for effect of incubation constancy on daily survival rate (DSR) of king eider nests found at Teshekpuk and Kuparuk, Alaska, USA, 2002–2005. Factors in models included site, observer effect, and incubation constancy.

| DSR model | <i>K</i> ^a | AIC _c ^b | Δ AIC _c ^c | w_i ^d | Deviance |
|--------------------------------------|-----------------------|-------------------------------|--|--------------------|----------|
| Site, observer | 3 | 152.05 | 0 | 0.73 | 146.04 |
| Site, observer, incubation constancy | 4 | 154.03 | 1.98 | 0.27 | 146.02 |
| (.) | 1 | 162.4 | 10.34 | 0 | 160.39 |
| Incubation constancy | 2 | 164.14 | 12.09 | 0 | 160.14 |

^a No. of parameters in the model.

^b Akaike's Information Criterion adjusted for small sample size.

^c Difference between model AIC_c and AIC_c value of the best model.

^d AIC_c wt.

the range detected. Incubation constancy varied from 70% to 100% but most females maintained constancy at 98% (R. L. Bentzen, unpublished data). King eiders rely primarily on endogenous reserves during incubation (Lawson 2006; Bentzen et al., in press) and have likely reduced variation in incubation constancy as much as possible, thereby limiting detrimental effects of cooling, movement to and from the nest, scent trails, and absence from the nest associated with incubation recesses. We suggest that high incubation constancy is the result of past selection but does not currently play a large role in nest survival at an individual level.

In summary, factors influencing king eider nest success were complex. We suggest that king eiders are caught between competing predation pressures associated with 2 primary predators, avian and mammalian. It appeared king eiders may use a concealed breeding strategy as females seemed to derive some benefit from nesting in areas with more willow on days when the nest was visited by observers, likely due to avian predation pressures. The overall negative effect of increased cover may be driven by mammalian predators preferentially foraging in these areas. We found no evidence that king eiders employ secluded nesting strategies or that they benefit from increased incubation constancy.

MANAGEMENT IMPLICATIONS

The king eider population has declined in recent decades (Suydam et al. 2000) and the underlying causes are unknown. King eiders were negatively impacted by observers near the nest, although females were rarely flushed on revisits, and using nest survival estimates without considering observer effects could result in misleading conclusions. Therefore, we recommend future studies take every precaution to limit effects of nest visits and to consider them as a possible negative bias in estimated nest survival. The highest densities of king eiders in Alaska are within the National Petroleum Reserve-Alaska (W. Larned, United States Fish and Wildlife Service, unpublished report) which is >87% open for oil and gas leasing (Bureau of Land Management 1998, 2004). Future models of the impact of petroleum development on nest survival of tundra-nesting waterfowl should consider the influence of humans in the vicinity of nest.

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