

Strategies for Nest-Site Selection by King Eiders

REBECCA L. BENTZEN,¹ *Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775-7220, USA*

ABBY N. POWELL, *United States Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK 99775-7020, USA*

ROBERT S. SUYDAM, *North Slope Borough, Department of Wildlife Management, P.O. Box 69, Barrow, AK 99723, USA*

ABSTRACT Nest site selection is a critical component of reproduction and has presumably evolved in relation to predation, local resources, and microclimate. We investigated nest-site choice by king eiders (*Somateria spectabilis*) on the coastal plain of northern Alaska, USA, 2003–2005. We hypothesized that nest-site selection is driven by predator avoidance and that a variety of strategies including concealment, seclusion, and conspecific or inter-specific nest defense might lead to improved nesting success. We systematically searched wetland basins for king eider nests and measured habitat and social variables at nests ($n = 212$) and random locations ($n = 493$). King eiders made use of both secluded and concealed breeding strategies; logistic regression models revealed that females selected nests close to water, on islands, and in areas with high willow (*Salix* spp.) cover but did not select sites near conspecific or glaucous gull (*Larus hyperboreus*) nests. The most effective nest-placement strategy may vary depending on density and types of nest predators; seclusion is likely a mammalian-predator avoidance tactic whereas concealment may provide protection from avian predators. We recommend that managers in northern Alaska attempt to maintain wetland basins with islands and complex shorelines to provide potential nest sites in the vicinity of water. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):932–938; 2009)

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Breeding habitat selection is a critical component of reproduction in birds because it determines the environment to which the parents and eggs will be exposed for a long period of time and has presumably evolved in relation to predation, local availability of resources, and microclimate (Gloutney and Clark 1997). An individual's chance of reproductive success increases with the ability to choose a nest site that minimizes risk of predation to eggs, chicks, and attendant adults. Nest losses often constitute the greatest source of annual mortality in birds (Ricklefs 1969) and, therefore, any adaptations that increase nest success even slightly, such as nest-site choice, should have selective value (Ricklefs 1984). Predators are the most important selective force affecting nest success (Ricklefs 1969, Martin 1995), potentially resulting in a variety of strategies related to nest protection, including breeding synchrony (Imms 1990), coloniality (Wittenburger and Hunt 1985), distraction behavior (Lack 1968, Trivers 1972), aggressive nest defense (Edmunds 1974), and nest-site selection (Larson 1960, Crabtree et al. 1988, Kellett et al. 2003).

King eiders (*Somateria spectabilis*) typically choose nest sites that are dispersed across the tundra or on islands in tundra lakes throughout the circumpolar arctic (Kellett and Alisauskas 1997, Suydam 2000). Although little is known about king eider nesting habitats (Suydam 2000), avoidance of predators, primarily arctic foxes (*Alopex lagopus*), may drive nest-site selection (Larson 1960, Kellett et al. 2003). Larson (1960) argued that 2 main evolutionary strategies are used by arctic-nesting birds that have a limited ability to defend their nests: 1) secluded nesting, wherein success increases with greater inaccessibility of nest location, or 2) concealed nesting, wherein success increases with more concealed nest location. In most waterfowl, and eiders in

particular, the main option for secluded breeding is to nest on islands. The concealed breeding strategy relies on the nest and attendant female being camouflaged to some degree, usually by vegetation around the nest (Larson 1960).

Predators of king eider eggs are either avian (gulls [*Larus* spp.], jaegers [*Stercorarius* spp.], and common ravens [*Corvus corax*]) or mammalian (arctic fox; Lamothe 1973, Kellett 1999) and strategies to avoid predation likely vary by predator type. Incubating eiders are unable to defend their nests from foxes and do not feign injury to draw potential predators from the nest, suggesting that eiders should benefit from secluded nesting in the presence of arctic foxes (Larson 1960). However, king eiders have been known to successfully deter predation attempts by gulls on occasion (Kellett and Alisauskas 1997) and jaegers (Blomqvist and Elander 1988), thus most avian depredation occurs when incubating females are absent from their nests (Swennen et al. 1993). Therefore, to avoid avian predation it would be advantageous to maintain high incubation constancy and maximize nest concealment.

Nesting associations with conspecifics or other avian species may also be important to nest success. King eiders may defend their nests either individually or in cooperation with conspecifics (Kellett and Alisauskas 1997, Blomqvist and Elander 1988). Although generally considered solitary nesters, semicolonial nesting does occur in some locations (Kellett and Alisauskas 1997). Additionally, protection from both avian and mammalian predators may be gained by nesting in association with species that defend their own nests aggressively (Giroux 1981, Blomqvist and Elander 1988, Kellett and Alisauskas 1997, Quakenbush et al. 2004). King eiders sometimes nest in association with jaegers (Lamothe 1973, Blomqvist and Elander 1988), gulls (Götmark and Åhlund 1988), and terns (*Sterna paradisaea*; Kellett and Alisauskas 1997); however, the adaptive

¹ E-mail: frlm@uaf.edu

significance of these nesting associations is unclear because some of these species are also significant predators of eggs and ducklings (Dwernychuk and Boag 1972, Giroux 1981, Blomqvist and Elander 1988, Kellett and Alisauskas 1997).

The coastal plain of northern Alaska, USA, includes the entire breeding range of king eiders within Alaska (Suydam 2000) and is representative of king eider habitat across a larger scale. The highest densities of nesting king eiders in Alaska are within the northeast planning area of the National Petroleum Reserve-Alaska (NPR-A; W. Larned, United States Fish and Wildlife Service, unpublished report), which is 87% open for oil and gas leasing (Bureau of Land Management 1998). Oil and gas development can have impacts ranging from habitat loss to increased predation by foxes and gulls (Eberhardt et al. 1982, Truett et al. 1997, Burgess 2000, National Research Council 2003). Nest-site availability for tundra-nesting waterfowl on the coastal plain is also likely to be impacted by climate change. Knowledge of nest-site selection under current conditions is vital to evaluating and managing any future changes. Our goal was to evaluate social (distance to nearest conspecific nest and distance to nearest glaucous gull [*L. hyperboreus*] nest) and habitat (distance to water, % willow [*Salix* spp.] within 1 m, and island location) variables that may influence king eider nest-site choice on the coastal plain of northern Alaska. We hypothesized that nest-site selection is driven by predator avoidance (Kellett and Alisauskas 1997, Kellett et al. 2003) and that concealment and seclusion of nests is likely to affect nest placement.

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), 2003–2005 (Fig. 1). The Teshekpuk site was approximately 10 km south of the southeast shore of Teshekpuk Lake in the northeast planning area of the NPR-A and experienced minimal human impact (i.e., no roads, communities, or development for petroleum extraction). The Kuparuk study site was between the Colville and Kuparuk River deltas, within a site developed for petroleum production, and had associated road networks and human activities. Both 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 (*Carex* spp.) and pendant grass (*Arctophila fulva*) on the margins of lakes and ponds (Anderson et al. 1999). Dwarf willow (<40 cm in ht) was the dominant shrub and the main source of cover for nesting waterfowl.

METHODS

Habitat selection analysis can be greatly influenced by the extent of the study area chosen to represent available habitat (McClellan et al. 1998, Huston 2002); thus, we searched both study areas for eider nests in 2002, prior to this study. Based on this preliminary study, we considered wetland basins (Jorgenson et al. 2003a) as available habitat for nesting king

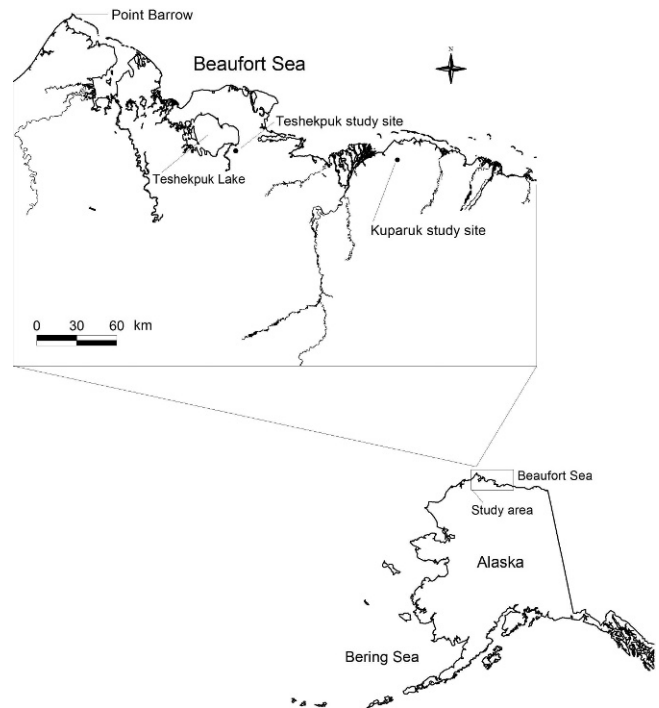


Figure 1. Locations of Kuparuk and Teshekpuk study areas of king eider nest-site choice (2003–2005) on the coastal plain of northern Alaska, USA.

eiders. Additionally, an earlier study done at a larger spatial scale indicated that king eiders selected vegetation classes associated with lakes and ponds and avoided vegetation classes at well-drained sites on Alaska's coastal plain (John Payne, Ducks Unlimited Inc., unpublished data). Near Teshekpuk, wetland basins were often adjacent to each other, but ranged from 1 km to 4 km apart at Kuparuk. In addition, we were able to search a larger area at Kuparuk (approx. 25 km² vs. 18 km² at Teshekpuk) because of road access there. We systematically searched wetland basins for king eider nests on foot, approximately 14 June through approximately 4 July at both sites and in all years (2003–2005). We searched all wetlands at least twice to account for females that initiated later than average and because of lower nest-detection probabilities during egg-laying. Edges of wetland basins were delineated by either low bluffs or dry tussock tundra. The farthest distance from water that we searched was 400 m. We marked nests with a tongue depressor placed 1 m away and concealed in vegetation. We recorded latitude and longitude of all king eider and glaucous gull nests using a handheld Global Positioning System unit.

We generated random points within wetland basins using the Random Point Generator 1.3 extension for ArcView Geographic Information System. We classified nests and random locations as island or mainland after most nests had hatched (15–28 Jul). We defined islands as sites where we had to cross any depth (>5 cm) and distance of water to reach them and if the island was large enough for a king eider nest. We recorded distance to nearest permanent water and percent cover by willow within 1 m of nests and random locations after hatch. We calculated distances to the nearest

glaucous gull and king eider nests using the spatial join function of the Geoprocessing Wizard extension in ArcView. Wetlands were largely snow-free prior to initiation of egg laying, although deeper ponds and lakes still contained considerable ice cover, and glaucous gulls were present on their territories prior to king eider nest initiation.

In 2004 and 2005 we visited an additional set of random locations (generated by the Random Point Generator) located in areas with a high concentration of islands, to boost the sample size of islands as random points and investigate characteristics of islands selected by king eiders. For nests and random points located on islands, we measured island length, distance to mainland, and depth of water at the deepest point of the shallowest route between the island and the mainland. All aspects of our field work were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (UAF IACUC 05-29).

Data Analysis

Because little is known about nest-site selection for king eiders, we developed 46 a priori models to investigate social and habitat factors that might influence nest-site selection. Our candidate model set examined effects of distance to water (water), percent willow within 1 m (willow), distance to nearest king eider nest (conspecific), island or mainland nest location (island), and distance to nearest glaucous gull nest (gull). We included all possible 1-, 2-, and 3-variable models using combinations of the variables to investigate social and habitat aspects of nest-site selection (e.g., model_{water}; model_{water+willow}; model_{water+willow+conspecific}; models no. 1–25). We hypothesized that effects of these variables may vary between sites, so we included all 2-variable additive models using combinations of the habitat and social variables and site (e.g., model_{water+site}; models no. 26–30) and 3-variable multiplicative models including interactions with site (e.g., model_{water+site+water×site}; models no. 31–35). Additionally, nest-site selection may vary between years due to variation in spring weather, predator abundance, or other unknown factors, and so we included all 2-variable additive combinations of the habitat and social variables and year (e.g., model_{water+yr}; models no. 36–40); we did not include any interactions with the variable year to limit the number of models in the candidate model set. We included 4 models with quadratic terms for water, willow, conspecific and gull (e.g., model_{water+water²}; models no. 41–44) because the relationship between continuous predictor variables and nest selection may not be linear. Lastly, we included a 5-variable additive model including all habitat and social variables (model_{water+willow+conspecific+island+gull}; model no. 45) and the null model (model no. 46).

As a separate analysis, we developed 13 a priori models describing nesting island selection by king eiders in 2004 and 2005. We compared characteristics of islands on which eiders nested to a random sample of islands within the study area. The candidate model set included the variables length of the island (length; index of island size), distance to the

mainland (distance; index of island isolation), and depth of water (depth; index of island isolation). We examined all 1- and 2-variable models (e.g., model_{length}; model_{length+distance}; models no. 1–6), multiplicative combinations of these variables (e.g., model_{length+distance+length×distance}; models no. 7–9), and quadratic terms (e.g., model_{length+length²}; models no. 10–12). Lastly we included a null model (model no. 13).

We used logistic regression (Allison 2000; SAS Institute, Cary, NC) to fit models and used the second-order Akaike's Information Criterion (AIC_c) to identify the most parsimonious model and predict variable importance (Burnham and Anderson 2002). We did not find any evidence of overdispersion; thus, we did not use a quasi-likelihood adjustment to AIC_c (QAIC_c). Logistic regression was an appropriate tool to analyze our use–availability study design (nests and random locations) because king eider nests are relatively easy to spot and infrequent on the landscape; therefore, we assumed available units were likely to include few undetected nests. However, nests that failed early, leaving only a swirl of dead grass, may not have been detected. Because use–availability study designs are approximately equivalent to case–control designs when use is rare (Keating and Cherry 2004, Johnson et al. 2006), we could estimate approximate odds ratios. We acknowledge that our data may not be truly independent if there was strong nest-site fidelity among years. Because this was an unmarked breeding population we were unable to determine whether females nested close to the previous year's nest; however, we do know they did not reuse the same nest bowl (R. L. Bentzen, University of Alaska Fairbanks, unpublished data). Modeling each year separately would decrease our sample size, so we modeled all years simultaneously but included year as a potential explanatory variable. We did not detect any multicollinearity among covariates, adjusted by the weight matrix used in the maximum likelihood algorithm (Allison 2000). We tested the top candidate model with the Hosmer–Lemeshow goodness-of-fit test statistic to ensure model fit (Hosmer and Lemeshow 1989).

We calculated Akaike weight (w_i) for each model, representing probability of that model as the best model in the set of candidate models (Burnham and Anderson 2002). We calculated the sum of model weights (Σw_i) for each variable using weights of all models that contained that variable. We used model-averaged parameter estimates and unconditional standard errors averaged over all models that contained a variable to determine the importance of that variable within the candidate set of models. We calculated odds ratios from averaged parameter estimates that represented the increase in probability of a site being used as a nest for every unit increase in the predictor variable (Allison 2000). We estimated probability of use (Manly et al. 2002) at 90% of the observed range of variables to present a range of variation relative to the true amount of variation in the data. We used model-averaged parameter estimates and held other variables at mean values. We report values as means \pm standard error.

RESULTS

We assessed habitat and social variables at 212 king eider nests and 493 random locations and at an additional 232 randomly selected islands. We found 33–34 nests/year at Kuparuk and 34–40 nests/year at Teshekpuk. The earliest nests were initiated the first week in June each year, with average laying dates of 17 June (± 0.6 days) at Kuparuk and 19 June (± 0.4 days) at Teshekpuk. We observed arctic fox, glaucous gulls, and parasitic (*S. parasiticus*) and long-tailed (*S. longicaudus*) jaegers depredating nests. Ravens, red fox (*Vulpes vulpes*), and golden eagles (*Aquila chrysaetos*) were also present on both study areas.

Nests were closer to water ($\bar{x} < 7$ m) and in areas with higher percentage of willow ($\bar{x} > 11\%$) than were random locations ($\bar{x}_{\text{water}} > 24$ m, $\bar{x}_{\text{willow}} < 6\%$). Nests and random locations were both far from the closest gull or conspecific nest ($\bar{x} > 400$ m). Of the subsample of nests and random points on islands, those at Kuparuk occurred on smaller islands ($\bar{x} < 51$ m), nearer the mainland ($\bar{x} < 57$ m), and in slightly deeper water ($\bar{x} > 37$ cm) than those at Teshekpuk ($\bar{x}_{\text{length}} > 107$ m, $\bar{x}_{\text{distance}} > 124$ m, $\bar{x}_{\text{depth}} < 29$ cm; Table 1).

The best-approximating a priori model describing king eider nest-site choice included the variables water, conspecific, gull, willow, and island ($\text{AIC}_c = 653.0$, $w_i = 0.51$, no. of parameters [K] = 6), and was 0.1 AIC_c units from the next best model, which did not include conspecific or gull ($\text{AIC}_c = 653.1$, $w_i = 0.49$, $K = 4$). These 2 models were 39 AIC_c units from the third-best model (model_{willow+island+conspecific}; $\text{AIC}_c = 692.0$, $w_i = 0.00$, $K = 4$) and 211.1 AIC_c units from the null model ($\text{AIC}_c = 864.2$, $w_i = 0.00$, $K = 1$). The Hosmer and Lemeshow goodness-of-fit test indicated that variables in the top model fit the logistic model ($\chi^2_8 = 14.5$, $P = 0.07$). Because the top 2 models carried all the weight ($\Sigma w_i = 1.0$), we effectively calculated model-averaged results from only the top 2 models. Model-averaging indicated that the odds of a site being selected for a nest were 4% lower with each 1-m increase of distance to water (odds ratio = 0.96) and 6% higher with each 1% increase in willow near the nest (odds ratio = 1.06). Odds of nest-site selection increased 6.1-fold for island versus mainland locations (odds ratio = 6.11). Although the variables conspecific and gull were included in the top model, they were not in the second-best model ($\Delta\text{AIC}_c =$

0.1), and odds of a site being selected for a nest did not vary for either (odds ratio = 1.00; Table 2). The variables site and year carried no weight ($\Sigma\text{AIC}_c \text{ wt} = 0$) and did not occur in models within 66 AIC_c units of the top model, indicating that the same relationships existed across sites and years.

The best-approximating model describing choice of islands for nest locations included the variables length, distance, and their interaction ($\text{AIC}_c = 312.4$, $w_i = 0.72$, $K = 4$) and was 3.7 AIC_c units from the next best model (model_{length+distance}; $\text{AIC}_c = 316.1$, $w_i = 0.11$, $K = 3$). The third best model was 4.4 AIC_c units from the top model (model_{length+length2}; $\text{AIC}_c = 316.8$, $w_i = 0.08$, $K = 3$); the top 3 models included 92% of combined model weights. The null model ($\text{AIC}_c = 320.2$, $w_i = 0.02$, $K = 1$) was only 7.8 AIC_c units from the top model. Distance to the mainland averaged 108.07 m, depth of water 32.67 cm, and island length 68.96 m on random islands across the 2 study areas. Model-averaged results indicated that estimated probability of use varied from 0.10 for a 0.5-m-long island (lower 90% observed range) to 0.27 for a 300-m-long island (upper 90% observed range). Estimated probability of use varied from 0.58 to 0.33 as distance from mainland increased from 1 m to 500 m and varied very little as depth of water increased from 5 cm to 100 cm (0.13–0.13; Table 3). Although there was some support for a quadratic effect of length, odds of an island being selected for a nest site did not vary with the quadratic term (parameter estimate < 0.001 , odds ratio = 1.00). The goodness-of-fit test indicated that variables in the top model adequately fit the data ($\chi^2_8 = 7.5$, $P = 0.48$).

DISCUSSION

King eiders selected nest sites on islands, near water, and in areas with greater willow cover, suggesting that eiders utilize strategies of concealment and seclusion. However, we found little evidence that king eiders choose nest sites based on nesting associations with either conspecifics or glaucous gulls.

Nesting on islands is likely an avoidance tactic for mammalian predators, because islands do not provide protection from avian predators such as gulls and jaegers. At Karrak Lake, Canada, Kellett et al. (2003) found that king eiders selected nest sites on more isolated islands

Table 1. Mean and standard deviation of variables measured at king eider nests ($n_{\text{Teshekpuk}} = 112$, $n_{\text{Kuparuk}} = 100$) and random sites ($n_{\text{Teshekpuk}} = 214$, $n_{\text{Kuparuk}} = 279$; 2003–2005), and at island nests ($n_{\text{Teshekpuk}} = 36$, $n_{\text{Kuparuk}} = 31$) and random sites on islands ($n_{\text{Teshekpuk}} = 123$, $n_{\text{Kuparuk}} = 109$; 2004–2005) at Teshekpuk and Kuparuk, Alaska, USA.

Variables	Teshekpuk				Kuparuk			
	Nests		Random		Nests		Random	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Distance to water (m)	6.9	11.7	23.6	54.5	2.6	10.7	26.8	37.5
Willow within 1 m (%)	16.3	20.4	6.2	9.6	10.6	10.2	6.4	8.9
Nearest gull nest (m)	928.9	880.2	1,133.6	695.4	581.1	840.7	967.2	1,133.5
Nearest conspecific nest (m)	444.8	425.0	640.8	371.8	740.9	1,050.9	1,119.7	1,395.1
Island length (m)	183.4	367.3	106.5	320.4	50.6	71.7	26.6	46.8
Distance to mainland (m)	124.3	173.5	153.6	202.8	39.0	54.7	56.7	95.6
Water depth (cm)	27.1	22.9	28.5	25.5	47.9	26.6	37.3	32.6

Table 2. Model-averaged parameter estimates, unconditional standard errors, odds ratios, and sum of Akaike weights (Σw_i) for variables found in logistic regression models of king eider nest-site selection at Teshekpuk and Kuparuk, Alaska, USA, 2003–2005.

Variable	Estimate	SE	Odds ratio	Σw_i
Distance to water	-0.037	0.008	0.964	1.000
% willow within 1 m of nest	0.061	0.010	1.063	1.000
Island or mainland location	1.809	0.222	6.105	1.000
Distance to conspecific nest	0.000	<0.001	1.000	0.508
Distance to glaucous gull nest	0.000	<0.001	1.000	0.508

(further from the mainland) and experienced higher nest success (30–89%) than reported for mainland populations in other areas (0–22%, Lamothe 1973; 21–57%, Bentzen et al. 2008). However, it was an exclusively island-nesting population, occurring within a large lesser snow (*Chen caerulescens*) and Ross's goose (*C. rossii*) colony, and islands were surrounded by relatively deep water (Kellett and Alisauskas 1997). King eiders nesting on Alaska's coastal plain on mainland tundra and shallow-water islands did not experience higher nest survival at secluded (island) nest sites (Bentzen et al. 2008). Additionally, we did not find any preference for more isolated islands, potentially due to a lack of truly isolated islands on the coastal plain, and only weak evidence for selection of larger islands. King eiders nesting in areas with only shallow-water tundra ponds (which characterizes much of their circumpolar range) may not have had a viable option for secluded nesting. Without truly secluded nest sites, low densities of foxes or abundant alternative prey such as lemmings (*Lemmus* spp. or *Dicrostonyx* spp.) or goose eggs leading to decreased predation pressure by foxes may be required for successful breeding (Bêty et al. 2001).

King eiders nesting on Alaska's coastal plain apparently selected for nest concealment; however, the consequences of nesting in a concealed location may be mixed. Although many studies have examined the relation between nest success and concealment, the interaction remains unclear. Some studies demonstrated a benefit (Odin 1957, Jones and Hungerford 1972, Crabtree et al. 1988), whereas others did not (Jessen et al. 1964, Dwernychuk and Boag 1972, Thorton 1982). We found that when disturbed by observers, king eider nests with more cover had higher nest success than those nests with lower cover, likely due to avian predation while the nest was unattended; however, increased concealment at the nest actually reduced nest survival when the nest was undisturbed, potentially due to foxes focusing on foraging in areas with willow cover as the most efficient habitat for hunting (Bentzen et al. 2008).

Table 3. Model-averaged parameter estimates, unconditional standard errors, odds ratios, and sum of Akaike weights (Σw_i) for variables found in logistic regression models of king eider island nest-site selection at Teshekpuk and Kuparuk, Alaska, USA, 2004–2005.

Variable	Estimate	SE	Odds ratio	Σw_i
Island length	0.004	0.002	1.004	0.935
Distance to mainland	-0.002	0.001	0.998	0.850
Depth water	0.001	<0.001	1.000	0.051

In contrast to king eiders nesting at other locations, eiders in northern Alaska selected sites that were very close to water (approx. 5 m); nests at Karrak Lake, Canada averaged 24 m from water (Kellett and Alisauskas 1997), whereas those at Bathurst Island, Canada, averaged 594 m from water (Lamothe 1973). Choosing a nest site close to water is not an absolute requirement for king eiders because females can take off from land; however, it may provide either a quicker escape route or better access to food. Both predation pressure and availability of water likely differed between the Alaskan and Canadian sites, potentially influencing nesting strategy. King eiders studied at Karrak Lake nested exclusively on islands in deeper water (approx. 1.2 m; Kellett and Alisauskas 1997) and, therefore, had better protection from mammalian predators, potentially lessening the need for a quick escape route. However, eiders nesting on Bathurst Island were dispersed over open tundra with arctic fox in the vicinity (Lamothe 1973). An absence of secluded nest sites may lead to greater benefits of concealment, and nesting far from water may decrease the likelihood of fox predation if foxes target near-water habitats (Lecomte et al. 2008). Because nests on islands were only slightly closer to water (2.4 m \pm 0.7) than those on the mainland (7.3 m \pm 1.4), we do not feel that selection for proximity to water is simply a byproduct of strong selection for island nest sites.

Although king eiders have been suggested to nest in association with terns (Kellett and Alisauskas 1997), jaegers (Lamothe 1973, Blomqvist and Elander 1988), and gulls (Götmark and Åhlund 1988), more recent studies have not found these associations (Kellett et al. 2003, this study). We did not find any evidence that king eiders selected nest sites near glaucous gulls and in a parallel study found that nest survival was not affected by proximity to glaucous gull nests (R. L. Bentzen, unpublished data). A beneficial nesting association requires the aggressive nest defender initiate territory defense prior to nest selection by king eiders and have the ability to deter other predators, while king eiders must be able to avoid predation by their associates. Glaucous gulls were present on their territories prior to king eider nest initiation, giving eiders the choice as to whether to associate. However, jaegers and gulls eat eider eggs (Lamothe 1973, Kellett and Alisauskas 1997), can displace eiders from their nests (R. L. Bentzen, unpublished data; P. Flint, United States Geological Survey, unpublished data), take eggs during incubation breaks (Swennen et al. 1993), and may not be able to keep arctic foxes out of their own territories (Larsen and Grundetjern 1997), thus limiting potential benefits of nesting associations to king eiders. Nest

associations reported by other researchers may have been confounded with habitat associations where both species selected the same nest habitat; social and habitat nest associations may be difficult to separate. Alternatively, in some cases nesting associations may be serendipitous in that both waterfowl and their associates may nest at high numbers or experience high nest success in years when an alternative prey, such as lemmings, are abundant. During our study, lemming populations were low and invariant (R. L. Bentzen, personal observation), possibly limiting our ability to detect beneficial nesting associations (Béty et al. 2001).

Nest-site selection did not vary between sites or among years, indicating that the same relationships existed across both despite some differences between study areas. The most effective nest-placement strategy may vary depending on predator density and type; seclusion is likely a mammalian-predator avoidance tactic whereas concealment could provide protection from both mammalian and avian predators. However, predator densities and assemblages (Callaghan et al. 2004, Pamperin et al. 2006), shrub cover (Sturm et al. 2001), and wetland configuration and formation on the coastal plain are changing (Jorgenson et al. 2003b, Hinzman et al. 2005), leading to unknown impacts on nest-site choice and nest survival of king eiders. Uncertainty associated with climate change is likely to exacerbate the uncertainty in our understanding of the costs and benefits of nest-site choice.

MANAGEMENT IMPLICATIONS

The highest densities of king eiders in Alaska are within the National Petroleum Reserve-Alaska (W. Larned, unpublished report), of which >87% is open for oil and gas leasing (Bureau of Land Management 1998, 2004). To mitigate impacts of future development on eider populations, we recommend that managers on the coastal plain of northern Alaska attempt to maintain nesting habitat in wetland basins with complex structure (islands and peninsulas), thereby maximizing potential nest sites near water. Additionally, changes in breeding habitat through climate warming such as changes in shrub cover, timing of snow and ice melt, wetland hydrology, and predictability (Hinzman et al. 2005) may impact future nest-site availability and nest-site choice for tundra-nesting waterfowl as well as the abundance of their associated predators. We suggest that further research focusing on costs and benefits of nest-site choice, and on predator-prey interactions between foxes and eiders, is vital for our understanding and ability to manage this system.

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