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NEST-SITE SELECTION, INTERSPECIFIC ASSOCIATIONS, AND NEST SUCCESS OF KING EIDERS

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Abstract. We investigated factors influencing nest success in King Eiders (*Somateria spectabilis*) at Karrak Lake, Nunavut, Canada, during 1995–2001. Island-nesting King Eiders had higher nest success (range 30–89%) than that reported for mainland-nesting populations, and nested at much higher densities (46–198 nests km^{-2}) than on mainland, where they were detected infrequently (usually <1 nest km^{-2}). Predation was the main cause of nest failure, and King Eider nest success was greater on isolated islands (smaller islands, and larger islands farther from the mainland) that were presumably less accessible to mammalian predators. King Eiders did not derive protection from predators by nesting near gulls (*Larus* spp.) and Arctic Terns (*Sterna paradisaea*).

Key words: interspecific nesting associations, island nesting, King Eider, nest success, Queen Maud Gulf Bird Sanctuary, Somateria spectabilis.

Selección del Sitio de Nidificación, Asociaciones Interespecíficas y Éxito de Nidificación de *Somateria spectabilis*

Resumen. Investigamos los factores que influencian el éxito de nidificación de *Somateria spectabilis* en Karrak Lake, Nunavut, Canada, durante 1995–2001. Los individuos que nidifican en las islas presentaron un mayor éxito de nidificación (entre 30–89%) que el reportado para las poblaciones que nidifican en el continente, y anidaron a una mayor densidad que en el continente, donde se detectaron infrecuentemente (usualmente <1 nido km^{-2}). La depredación fue la principal causa de fracaso, y el éxito de nidificación de *S. spectabilis* fue mayor en islas grandes y pequeñas más alejadas del continente, las que presumiblemente se encontraban menos accesibles a mamíferos depredadores. *Somateria spectabilis* no obtuvo protección contra depredadores al nidificar cerca de gaviotas (*Larus* spp.) y gaviotines *Sterna paradisaea*.

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King Eiders (*Somateria spectabilis*) are commonly assumed to nest primarily in low densities on mainland (i.e., large islands or continental land masses; reviewed by Suydam 2000). However, some studies have reported high densities of King Eiders nesting on islands in tundra lakes (Hanson et al. 1956, Kellett and Alisauskas 1997). Islands are visited infrequently by mammalian predators, so we predicted that nest success would be greater on islands than on mainland (Larson 1960, Laurila 1989). Also, King Eiders may respond adaptively to predators by selecting islands over mainland habitats for nesting (Clark and Shutler 1999). Among islands, we predicted that King Eiders nesting on small islands located farther from the mainland would experience greater success, and would select such islands for nesting. Further, King Eiders often share nesting islands with gulls (*Larus* spp.), Arctic Terns (*Sterna paradisaea*), and geese (*Chen* spp.; Dement'ev and Gladkov 1967, Kellett and Alisauskas 1997). We predicted that King Eiders nesting in proximity to aggressive species would experience higher nest success (Underhill et al. 1993, Summers et al. 1994, Cotter and Hines 2001). This paper expands and supplements data presented in Kellett and Alisauskas (1997); specifically to document the incidence, nest success, and sources of variation in nest success of island-nesting King Eiders.

METHODS

We studied Karrak Lake and Adventure Lake (67°14′N, 100°15′W), which are located 60 km south of Queen Maud Gulf, Nunavut, in the Queen Maud Gulf Bird Sanctuary of the central Canadian Arctic (Kellett and Alisauskas 1997). Karrak Lake is large (16.1 km^2, including 2.5 km^2 of islands) and shallow (ca. 1.2 m deep, but spring runoff raises water levels by >1 m). Adventure Lake is smaller (8.8 km^2, including 0.2 km^2 of islands) and deeper (approximately 2.5 m deep). Islands in both lakes consist of rock and gravel, and are sparsely vegetated.

We systematically searched all islands (n = 107) of Karrak (1995–2001) and Adventure (1996–2001) Lakes for King Eider nests beginning in mid-June, corresponding to laying and early incubation periods. We marked nest locations with small stakes 1 m from nests, and revisited nests every 2–7 days to determine clutch size and nest fate. Nests were most easily detected when females flushed from nests, but we also

TABLE 1. Logistic regression models for presence of King Eider nests on islands of Karrak, Adventure, and Simpson Lakes, Nunavut, Canada, during 1995–2001. Model parameters of size and distance refer to island size and distance of island to mainland, respectively. Models were evaluated using Akaike's Information Criterion adjusted for small sample size (AIC_c). The model with the lowest AIC_c is the best-approximating model. The difference between a given model and the best model is given by ΔAIC_c. We considered models with $\Delta AIC_c < 4.0$ equivalent in their ability to explain the data. Model weights indicate the likelihood of a given model and sum to 1. k = number of parameters.

Model	k	AIC_c	ΔAIC_c	Model weight
Size, Distance	4	100.94	0.00	0.19
Distance	3	101.74	0.80	0.13
Size, Distance^2	5	102.03	1.09	0.11
Size, Distance, Lake	6	102.04	1.10	0.11
Distance^2	4	102.27	1.34	0.10
Size, Distance, Size × Distance	5	102.34	1.40	0.10
Distance, Lake	5	102.67	1.73	0.08
Size, Distance^2, Lake	7	103.39	2.45	0.06
Distance^2, Lake	6	103.52	2.58	0.05
Size	3	104.40	3.46	0.03
Size, Lake	5	106.02	5.08	0.02
Lake	4	106.80	5.86	0.01

found failed nests and active nests in which the female was absent or did not flush. For this reason, we believe that detection of both active and failed nests was high. We recorded probable causes of nest failure (e.g., abandonment, depredation) and presence of nesting Arctic Terns, and Glaucous (*Larus hyperboreus*), Herring (*L. argentatus*), and Thayer's (*L. thayeri*) Gulls on islands with nesting King Eiders. We calculated initiation dates by backdating from known laying or hatch dates, or from estimated incubation stages determined by candling eggs (Weller 1956), assuming a laying interval of one egg day^{-1} (Lamothe 1973) and incubation length of 23 days (Parmelee et al. 1967).

To determine use of islands by King Eiders elsewhere in Queen Maud Gulf Bird Sanctuary, we visited each island of Simpson (67°15′N, 99°52′W), Big Island (67°28′N, 100°47′W), Pitok (67°02′N, 101°16′W), Franklin (67°04′N, 99°21′W), and Portage (67°08′N, 100°00′W) Lakes once in mid-July, 1997, and recorded clutch size and incubation stage (Weller 1956) of all nests. We also visited Simpson Lake in early to mid-July, 1998–2001, and recorded clutch sizes and incubation stages.

We digitized shorelines and islands of Karrak, Adventure, and Simpson Lakes from 1:50 000 maps, imported data into a Geographical Information System (GIS; Tydac Research Inc. 1997), and calculated size and distance of each island to the nearest mainland shore. Islands of these lakes were classified by general habitat. Class 1 and 2 islands were composed of mud and rock, respectively; both had little vegetation and often were submerged until early July. Class 3 islands consisted of rock, gravel, and vegetation, and remained largely exposed even during fluctuating water levels.

We conducted annual surveys of Lesser Snow (*Chen caerulescens*) and Ross's (*C. rossii*) Goose populations at Karrak Lake during mid-June to early July. Circular plots (range 111–189 plots year^{-1}) of 20-m (1995–1996) or 30-m (1997–2001) radius spaced at 0.5-km or 1.0-km intervals measured goose nesting density on mainland habitat, and we recorded occurrence of King Eider nests within these plots.

STATISTICAL ANALYSES

We used SAS (SAS Institute 1996) for all analyses. King Eiders used only class 3 islands for nesting; thus all analyses were restricted to those islands. We evaluated presence of King Eider nests with logistic regression (PROC CATMOD, SAS Institute 1996) using 12 candidate models involving combinations of island size, distance from island to mainland, lake, and interaction of island size and distance to mainland. PROC CATMOD models the probability of the first sorted value (SAS Institute 1996), so we multiplied parameter estimates by −1 so that slopes of parameter estimates could be conventionally interpreted. Islands with nesting King Eiders detected in one or more years were coded as "present," whereas islands without King Eiders in all years were coded as "absent." We used Akaike's Information Criterion with small sample size adjustment (AIC_c, Burnham and Anderson 1998) to choose best-approximating model(s). We used log-likelihood and error sum of squares values to calculate AIC_c using logistic regression and general linear models (see below), respectively (Burnham and Anderson 1998). Parameter estimates are denoted as $\theta \pm$ SE.

We estimated nest success for Karrak and Adventure Lakes following Mayfield (1975) and Johnson (1979). Annual mean clutch sizes (Table 1) multiplied by laying interval (1 egg day^{-1}, Lamothe 1973) were used as exposure lengths during laying. For failed nests, date of failure was assumed to have occurred at the midpoint between observations for intervals less than 15 days and at 40% for intervals greater than 15 days (Mayfield 1975, Johnson 1979). Nest success reported for Karrak Lake in 1995 differed from that reported by Kellett and Alisauskas (1997) which assumed date of failure to be predicted hatch date, resulting in overestimation of observed exposure days for failed nests.

We expressed island nest success as daily nest survival rate (Mayfield 1975, Johnson 1979) calculated for each island each year. General linear models (PROC GLM, SAS Institute 1996) were used to evaluate island daily survival rate using 73 candidate models involving combinations of island size, distance from island to mainland, gull density, Arctic Tern density, King Eider density, and year. We also included quadratic versions of the above variables and two-way interactions of distance from island to mainland and year, Arctic Tern density and King Eider density, gull density and King Eider density, and gull and Arctic Tern density in candidate models. AIC_c was used to choose best-approximating model(s). Normality of residuals of the full model was improved (indicated by Wilk-Shapiro test for normality, $W = 0.80$ to $W = 0.91$) by arcsine transforming daily survival rates, and so we did not calculate a variance inflation factor, $\hat{c}$. Although this transformation greatly improved normality, residuals were positively correlated with dependent variables, indicating there was substantial variation due to unknown factors that were not included in our model ultrastructure (Zar 1996).

RESULTS

We found 41 (Kellett and Alisauskas 1997), 52, 66, 73, 109, 113, and 131 nests on islands of Karrak Lake in 1995–2001, and 48, 57, 73, 82, 78, and 77 nests on islands of Adventure Lake in 1996–2001, respectively. We found 24, 22, 23, 14, and 18 nests on islands of Simpson Lake in 1997–2001, respectively. Islands of Franklin, Big Island, Pitok, and Portage Lakes yielded 1, 1, 7, and 9 active nests in 1997, respectively. However, numbers of nests at these lakes are likely underestimated, as these areas were visited during late incubation (mid-July) when we also found evidence of failed and hatched nests.

Not all islands were used by nesting King Eiders. We found nests on 10–16 of 77 islands of Karrak Lake (1995–2001), 11–15 of 30 islands of Adventure Lake (1996–2001), and 5–9 of 34 islands of Simpson Lake (1997–2001). For all years combined, King Eiders used only class 3 islands for nesting (68%, 55 of 81 islands).

The best-approximating logistic model describing King Eider nest presence on islands (Table 1, $AIC_c = 100.94$, $n = 81$, $k = 4$) included island size ($\theta = 19.0 \pm 14.1$ km^2) and distance from island to mainland ($\theta = 4.6 \times 10^{-3} \pm 2.2 \times 10^{-3}$ m). Competing models were similar in terms of AIC_c values (10 of 12 models tested had ΔAIC_c values <4.0), and most often included lake and an interaction between island size and distance to mainland. Islands with King Eider nests were farther from the mainland, but parameter estimates for all other variables included zero.

We searched 111–189 mainland goose nest plots during 1995–2001 and found only one King Eider nest; representing an annual range of densities of 0–2 nests km^{-2}. While traveling between mainland plots, we incidentally found very few nests (mean = 2.7, range 0–12). In contrast, densities of King Eider nests on islands ranged annually between 46 and 198 nests km^{-2}.

Nest success of island nesting King Eiders at Karrak and Adventure Lakes ranged from 30% to 89% (Table 2). Predation accounted for 66% ($n = 277$) of nest failures, most (84%, $n = 233$) being destroyed by unknown predators. We suspect arctic fox (*Alopex lagopus*), gulls, and jaegers (*Stercorarius* spp.) were responsible for most nest losses, as these species were commonly observed. Wolves (*Canis lupus*), wolverines (*Gula luscus*), grizzly bears (*Ursus horribilis*), and Common Ravens (*Corvus corax*) were seen on the study area much less often. Other causes of nest failure included abandonment (24%, $n = 100$), and observer influence (9%, $n = 36$; abandonment after capture of female), or rotten or infertile eggs (1%, $n = 3$). The risk of nest failure may be exacerbated by poor body condition; females may decrease incubation constancy to exploit available food sources, or abandon nests to increase probability of future reproductive success (Kellett and Alisauskas 2000).

The best-approximating model describing island nest success (Table 3, $AIC_c = -498.95$, $n = 164$, $k = 14$) included island size ($\theta = -2.6 \pm 0.9$ km^2, $r^2 = 0.04$), distance from island to mainland ($\theta = -6.4 \times 10^{-5} \pm 1.6 \times 10^{-4}$ m, $r^2 < 0.01$), year ($r^2 = 0.09$), Arctic Tern density ($\theta = -8.7 \times 10^{-5} \pm 3.8 \times 10^{-5}$ nests km^{-2}, $r^2 = 0.03$), gull density ($\theta = 2.5 \times 10^{-4} \pm 1.8 \times 10^{-4}$ nests km^{-2}, $r^2 = 0.03$), and an interaction between island size and distance to mainland ($\theta = 1.2 \times 10^{-2} \pm 4.7 \times 10^{-3}$, $r^2 = 0.04$). The top three competing models ($\Delta AIC_c < 4.0$) contained combinations of these variables plus an interaction between gull and Arctic Tern density ($\theta = 2.8 \times 10^{-7} \pm 9.3 \times 10^{-7}$, $r^2 < 0.01$). To explore the interaction between island size and distance to mainland, we divided island size into two classes (less than and greater than the median), and repeated the analysis for each group. For small islands, distance to mainland did not influence nest success ($\theta = 2.1 \times 10^{-5} \pm 1.6 \times 10^{-4}$ m), whereas nest success was higher on larger islands farther from the mainland ($\theta = 5.3 \times 10^{-4} \pm 2.3 \times 10^{-4}$ m). Thus, nest success was greater on smaller islands, on large islands farther from the mainland, and on islands with low densities of nesting Arctic Terns.

DISCUSSION

Presumably, birds should select nesting habitats that maximize reproductive success and survival (Larsen and Grundetjern 1997). At Karrak Lake, island-nesting King Eiders experienced higher nest success (30–89%; this study) than that reported for mainland-nesting populations (0–8%; Lamothe 1973; R. Bromley, pers. comm.). Thus, use of islands instead of mainland habitats could have been an adaptive response to predation (Clark and Shutler 1999). Further, King Eiders at Karrak Lake had greater nest success on more-isolated islands (small islands, and large islands farther from the mainland), and tended to use more isolated islands (farther from the mainland) for nesting. Similar patterns have been reported for Common Eiders (*Somateria mollissima*; Laurila 1989, Robertson 1995). In partial agreement, Kellett and Alisauskas (1997) reported greater nest success on islands farther from the

TABLE 2. Annual clutch sizes and Mayfield nest success of island-nesting King Eiders at Karrak and Adventure Lakes, Nunavut, Canada, 1995–2001.

Nest stage	Clutch size (± SD)	Exposure days	No. of failures	Total nests	Daily survival rate (DSR ± SE)	Mayfield nest success (%)	95% CI
1995							
Laying	5.4 ± 1.7	16	2	7	0.871 ± 0.085	47	15–100
Incubation		504	10	35	0.980 ± 0.006	63	47–84
Total						30	7–84
1996							
Laying	5.5 ± 1.4	16	0	13	1.000 ± 0.000	100	
Incubation		1591	8	97	0.995 ± 0.002	89	82–97
Total						89	82–97
1997							
Laying	5.8 ± 2.0	115	4	41	0.965 ± 0.017	82	66–100
Incubation		1616	48	112	0.970 ± 0.004	50	41–61
Total						41	27–61
1998							
Laying	5.3 ± 1.7	131	7	50	0.946 ± 0.020	75	60–93
Incubation		2168	53	133	0.976 ± 0.003	57	48–66
Total						42	29–61
1999							
Laying	5.0 ± 1.7	221	5	81	0.977 ± 0.001	89	80–99
Incubation		2618	74	173	0.972 ± 0.003	52	44–60
Total						46	36–60
2000							
Laying	5.0 ± 1.7	164	21	64	0.872 ± 0.026	50	37–67
Incubation		2755	40	156	0.986 ± 0.002	71	64–79
Total						36	24–54
2001							
Laying	5.0 ± 1.8	291	19	108	0.935 ± 0.015	71	61–83
Incubation		2318	58	140	0.975 ± 0.003	56	48–65
Total						40	29–54

TABLE 3. General linear models of island nest success of King Eiders nesting on islands of Karrak and Adventure Lakes, Nunavut, Canada, during 1995–2001, with corresponding AIC_c, ΔAIC_c, and model weights (as explained in Table 1). The best 10 of the 73 candidate models are presented. Model parameters of size, distance, gull, and tern refer to island size, distance of island to mainland, gull nest density, and tern nest density, respectively.

Model	k	AIC_c	ΔAIC_c	Model weight
Size, Distance, Year, $Gull^2$, Tern, Size × Distance	14	–498.95	0.00	0.29
Size, Distance, Year, Tern, Size × Distance	12	–497.65	1.30	0.15
Size, Distance, Year, $Gull^2$, Tern, Gull × Tern	15	–496.62	2.33	0.09
Size, Distance, Year, $Gull^2$, Size × Distance	13	–495.81	3.14	0.06
Distance, Year, $Gull^2$, Tern	12	–494.68	4.27	0.03
Size, Distance, $Gull^2$, Tern, Size × Distance	8	–494.57	4.38	0.03
Year, $Gull^2$, Tern	11	–494.35	4.60	0.03
Size, Distance, Year, Size × Distance	11	–494.17	4.78	0.03
Size, Distance, Year, $Gull^2$, Tern	13	–494.12	4.83	0.03
Size, Year, $Gull^2$, Tern	12	–493.89	5.06	0.02

mainland, but were unable to demonstrate that King Eiders selected such islands. They also reported that King Eiders nested only on medium-sized islands, but no relationship was found with island size and nest success. However, Kellett and Alisauskas (1997) presented only one year of data; we believe that the multiple years and improved analytical methods reported here are more robust.

Many arctic-nesting birds have higher nest success on mainland habitat when associated with aggressive species (Underhill et al. 1993, Summers et al. 1994, Tremblay et al. 1997). Such associations may be functionally similar to island nesting, as protective species may effectively repel terrestrial predators. Several studies have reported increased nest success from association with gulls (Burger 1984, Götmark and Åhlund 1988, Väänänen 2000), terns (Evans 1970, Young and Titman 1986), and conspecifics (Hötker 2000), and we predicted that island-nesting King Eiders at Karrak Lake would benefit from association with larids and conspecifics through deterrence of avian predators. Contrary to our expectations, however, we found no relationship between nest success and density of gulls or King Eiders, although Kellett and Alisauskas (1997) reported a correlation between nest success and numbers of conspecifics per island. Nest success was negatively correlated with density of Arctic Terns; either this relationship was spurious, or perhaps the highly visible activity of Arctic Terns attracted predators to nesting islands.

Whereas dispersed nesting on mainland areas could reduce density-dependent predation (Larsen and Moldsvor 1992, Larsen and Grundetjern 1997), aggregations of King Eiders on islands refute the notion that the species is intolerant of conspecifics nesting in proximity (Palmer 1975). In our study, islands were selected over mainland habitat for nesting, and nest success on islands was much higher than that reported for mainland areas, likely due to fewer mammalian predators. Further, although relationships were weak, nest success tended to be higher on isolated islands, and such islands were selected for nesting. Although other studies have demonstrated benefits of interspecific nesting associations, King Eider nest success in this study was largely unaffected by nesting near gulls and terns, and associations with larids could simply reflect similar nesting habitat preferences.

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SEX ROLES DURING INCUBATION IN THE COMMON RINGED PLOVER

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Abstract. Parental behavior during incubation is an important aspect of the breeding system, which varies greatly among shorebirds. There are, however, few studies of incubation sex roles in shorebirds during darkness. In *Charadrius* species, males are believed to perform most of the incubation during the night. In this study of night- and daytime incubation sex roles in the Common Ringed Plover (*Charadrius hiaticula*), males tended to do more of the nighttime incubation (58%) than did females; during the day the roles tended to be reversed (males 45%), but the differences were not statistically significant. The reasons why mates of the Common Ringed Plover seem to share nocturnal incubation more equally than do other *Charadrius* species are not clear but may involve differences in food levels and day length between areas.

Key words: Charadrius, *Common Ringed Plover, nocturnal incubation, sex roles, shorebirds, waders.*

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Papel de los Sexos durante la Incubación en *Charadrius hiaticula*

Resumen. El comportamiento parental durante la incubación es un aspecto importante del sistema reproductivo, el cual varía considerablemente entre las aves playeras. Sin embargo, los estudios sobre el papel de los sexos en la incubación nocturna en las aves playeras son escasos. En las especies de *Charadrius*, se cree que los machos realizan la mayor parte de la incubación nocturna. En este estudio, sobre el papel de los sexos durante los periodos de incubación nocturnos y diurnos en *Charadrius hiaticula*, los machos tendieron a realizar una mayor parte de la incubación nocturna (58%) que las hembras; durante el día los papeles tendieron a revertirse (machos 45%), pero las diferencias no fueron significativas estadísticamente. Las razones por las cuales las parejas de *C. hiaticula* parecen compartir más equitativamente la incubación nocturna que otras especies de *Charadrius* no están claras pero pueden estar relacionadas con diferencias en los niveles de alimento y duración del día entre áreas.