

CROSS-SEASONAL EFFECTS IN A SEA ICE-ASSOCIATED SEA DUCK: DO WINTER
CONDITIONS AFFECT BREEDING SPECTACLED EIDERS?

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Abstract

Climate change in the Arctic is more rapid than anywhere on the globe and changes in the marine environment can impact the distribution and abundance of Arctic and sub-Arctic species. Understanding how a species responds to climate change can aid conservation planning and recovery. Spectacled eiders (*Somateria fischeri*), sea ducks listed as “threatened” under the Endangered Species Act, winter at the Bering Sea and nest along the coastal areas of Alaska and Arctic Russia. Severity of winter conditions in the Bering Sea have been associated with both reduced annual survival and reduced breeding abundance and may have sublethal effects during the breeding season. In this study, we used 24 years of nesting data from Kigigak Island, a sub-Arctic site on the Yukon-Kuskokwim Delta, and 10 years from Utqiagvik, on the Arctic Coastal Plain, to examine the hypothesis that winter conditions in the Bering Sea influence the reproductive performance of eiders in the following breeding season. For both sites, we examined the effects of winter ice conditions and spring temperature and wind on nest initiation date, clutch size, and nest survival. Nest initiation date was not strongly associated with conditions experienced prior to the breeding season. Estimates of nest initiation date following extreme high and extreme low winter ice conditions differed by only 2 days. In contrast, the difference in mean initiation dates between sites was 20 days. We found no evidence that winter and spring conditions preceding the breeding season explained variation in clutch size (mean clutch size = 4.8, 95% CI: 4.7, 4.8), suggesting that breeding propensity may buffer against variation in clutch size. Nest survival varied among years; annual estimates ranged from 0.11 (95% CI: -0.02, 0.24) to 0.95 (95% CI: 0.92, 0.98) at Kigigak Island and 0.40 (95% CI: 0.16, 0.63) to 0.83 (95% CI: 0.66, 0.99) at Utqiagvik. At both sites, low days of high ice during winter were associated with lower nest survival and moderate to high counts of high ice cover

conditions during winter were associated with higher nest survival. After accounting for the effect of days of high ice during winter, nest survival was higher at Utqiagvik than Kigigak Island, potentially related to later nest initiation in the Arctic. We concluded that for breeding spectacled eiders, low sea ice winters are associated with reduced nest survival through reduced body condition, and we speculate that following winters with high sea ice more individuals may possibly decide not to breed. Delayed nest initiation at Arctic breeding sites may provide additional time for spectacled eiders to recover from low ice winters and contribute to higher nest survival at Utqiagvik compared to the sub-Arctic breeding site. Associations between changing ice conditions on multiple demographic rates may lead to future population declines for spectacled eiders at rates higher than previously predicted.

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1.1 Introduction

Marine ecosystems at high latitudes are being influenced by climate change, and some of the biggest impacts result from increasing temperature and altering the timing and extent of sea ice (Scavia et al. 2002, Mueter and Litzow 2008). The declining temporal and spatial extent of sea ice caused by rapid climate warming will likely cause declines in ice-dependent species. Some vertebrate species' life histories are associated with sea ice, and changes in sea ice may therefore affect their survival and reproduction (Marcogliese 2008, Lovvorn et al. 2009). For example, warming in the Arctic has resulted in changes in the abundance of primary consumers (Grebmeier 2012), which has affected the distribution of species that feed on benthic prey (Duffy-Anderson et al. 2019). The impact of variation in environmental conditions in the non-breeding season can carry-over into subsequent seasons of a species' annual cycle (Sedinger and Alisauskas 2014). Thus, understanding variation in a population parameter such as breeding success may require exploring environmental conditions experienced during other parts of a species' annual cycle.

Many migratory waterfowl species experience different climate conditions throughout the year as they migrate between and reside in their wintering, breeding, and molting areas. The conditions experienced during one season can have subsequent effects in the following season. If such effects influence individual fitness, they are called carry-over effects; if they influence population dynamics of a species, they are called cross-seasonal effects (Harrison et al. 2011, Sedinger and Alisauskas 2014). Several studies examining conditions that migratory birds experience during the non-breeding season have found carry-over effects in breeding success and egg laying dates (Schamber et al. 2012, Raquel et al. 2019).

Spectacled eiders (*Somateria fischeri*) are inextricably linked to the Bering Sea ecosystem in the sub-Arctic. This sea duck species spends only 3 months, at most, in terrestrial habitat during which it breeds along the coastal habitat in western and northern Alaska and Arctic Russia (Petersen et al. 1999). The Yukon-Kuskokwim Delta (YKD) hosts the highest density breeding area for spectacled eiders in North America (Dau and Kistchinski 1977), in contrast to much lower nest densities on the Arctic Coastal Plain (ACP) (Amundson et al. 2019). Starting in early spring (May on the YKD and mid-June on the ACP), spectacled eiders arrive in pairs at their breeding grounds. Male spectacled eiders remain until midway through the incubation period and then return to the sea for the remainder of the year (Petersen et al. 1999). Successfully breeding females remain on the breeding grounds an additional 2 months until their eggs have hatched and ducklings fledged, after which they migrate back to the sea with their broods in late August. Unsuccessful females return to the sea shortly after their clutch has been destroyed (Flint et al. 2000). During the other 9 months of their annual cycle, spectacled eiders reside in the marine environment, either in coastal habitat used for molting and staging, or in the north central Bering Sea, where individuals from all 3 breeding areas winter together (Petersen et al. 1998, 1999). Given their reliance on marine habitat for most of the year, ocean conditions have the potential to affect spectacled eider breeding performance.

In the 1970s the breeding population of spectacled eiders on the YKD decreased from ~48,000 to ~2,500 nesting pairs, triggering the species to be listed as “threatened” under the Endangered Species Act in 1993 (Stehn et al. 1993, USFWS 1993). No long-term data existed for numbers of spectacled eiders breeding on the ACP or Arctic Russia at the time of listing. Factors suspected of contributing to the decline on the YKD include exposure to contaminants, including exposure to lead from spent shotgun shell pellets on their breeding grounds, predation

during the breeding season, hunting pressure, and changes in the non-breeding habitat, which at the time was poorly understood (Franson et al. 1995, Grand et al. 1998, Flint et al. 2016, Christie et al. 2018).

Winter conditions influence the survival, abundance, and nesting success of spectacled eiders breeding on the YKD. Peterson and Douglas (2004) found an association between abundance of spectacled eiders counted during annual springtime surveys of the YKD between 1988 – 2002 and conditions during the preceding winter, specifically the additive effects of spring temperature, spring wind speed, and the number of days of high ice cover in the core wintering area used by spectacled eiders. Flint et al. (2016) found a negative association between annual apparent survival of spectacled eiders breeding at Kigigak Island from 1994 to 2004 and an index of ice severity that takes into account periods with consecutive days of ice cover on the Bering Sea wintering area. Christie et al. (2018) analyzed apparent survival of spectacled eiders at Kigigak Island between 1994 and 2015 and found support for a non-linear relationship between apparent survival and a count of days of high ice on the wintering area with a negative association between survival and ice following both high and low ice winters, although very few winters of low ice occurred over the period they studied. Using an integrated population model and data from Kigigak Island between 1993 – 2015, Dunham et al. (2021) found a similar non-linear association between apparent hatching success of nests and days of high ice cover on the wintering area, although this was driven by just one year of very low hatching success.

Mechanisms potentially underlying carry-over and cross-seasonal effects in spectacled eiders may be similar to those hypothesized to cause effects on adult survival, which are thought to be related to available foraging habitat, energy expenditure, and body condition. High ice conditions may increase energy demands during periods of extreme cold as reduced availability

of open leads in pack ice reducing access to benthic prey (Petersen and Douglas 2004, Flint et al. 2016, Christie et al. 2018). Associations with cold temperature and high wind during spring may be related to persistence of ice on the wintering area (Petersen and Douglas 2004). Low ice conditions, on the other hand, can result in rougher sea conditions and may affect spectacled eiders through the increased energy cost of constant swimming without the presence of sea ice used for roosting and dampening waves (Lovvorn et al. 2014). Any mechanism associated with reduced survival may also have consequences via reduced body condition in eiders going into the breeding season.

Cross-seasonal and carry-over effects in spectacled eiders may also have sub-lethal consequences. In most waterfowl species it is important for breeding females to store endogenous reserves prior to the breeding season that they use for egg formation and incubation (Sedinger and Alisauskas 2014). Winter conditions that prevent spectacled eiders from obtaining enough food resources may result in poor female body condition. Poor body condition, in turn, may affect timing of nest initiation through the time required to recover from a harsh winter, as well as clutch size and egg hatching success through the amount of energy reserves females can use to produce eggs and meet their energy demands of egg incubation.

In this study, we examined the association between sea ice cover on the wintering ground along with spring wind and temperature to the reproductive performance of spectacled eiders using two long-term data sets: 24 years of data (1994 – 2015, 2019, 2021) from Kigigak Island, on the YKD of western Alaska, and 10 years of data (2010 – 2019) from Utqiagvik on the ACP of Alaska. Our objective was to examine the hypothesis that winter conditions in the Bering Sea influence the breeding performance of the spectacled eiders in the following breeding season. We examined the association between Bering Sea conditions during winter and spring (winter is

defined as 01 November – 31 March and spring is defined as 01 April – 30 April), and each of three response variables: (1) nest initiation date, (2) clutch size, and (3) nest daily survival rate (DSR) of spectacled eiders. We predicted these response variables would show patterns in their associations with conditions in the Bering Sea similar to those found in abundance and survival, reflecting sublethal effects of winter conditions on breeding performance.

1.2 Methods

1.2.1 Study Areas

The U.S. Fish and Wildlife Service (USFWS) collected data on breeding spectacled eiders at two coastal sites in Alaska: Kigigak Island and Utqiagvik. Kigigak Island (60°50' N, 165°50' W) is located on the coast of Yukon Delta National Wildlife Refuge, Alaska, USA, bordered by the Ninglick River to the northeast, Baird Inlet to the southeast and the Bering Sea to the west. The island contains 32.5 km² of low elevation tundra and is < 1 km from the coast. The island encompasses many open shallow ponds and tidally influenced sloughs. It supports a diverse community of nesting birds including shorebirds, gulls and terns (family Laridae), and a high concentration of many waterfowl species including cackling goose (*Branta hutchinsii minima*), greater white-fronted goose (*Anser albifrons*), emperor goose (*Anser canaagicus*), black brant (*Brant bernicla nigricans*), tundra swan (*Cignus columbianus*), northern pintail (*Anas acuta*), and spectacled eiders (Moran 2000, Christie et al. 2018). Habitat on Kigigak Island consists predominantly of low elevation tundra with sedge-graminoid meadows and a small amount of upland tundra near the center of the island. In the early spring or late fall there can be storm surges that inundate the low-lying areas on the island (Terenzi et al. 2014).

Utqiagvik (71°18' N, 156°40' W) is located at the Arctic Coastal Plain at the northern most tip of Alaska. The ACP is expansive and predominantly made up of dry tundra with many

open ponds and lakes. The buildings, roads, and gravel pads in and around Utqiagvik have created many waterbodies through the thawing of permafrost (Graff 2016). Some areas of tundra away from human influence are also depressed from the thawing of permafrost known as thermokarst subsidence, creating bodies of water (Lewis et al. 2012). Within the vicinity of Utqiagvik there are two sea duck species listed under the Endangered Species Act that breed in the area: Steller's eider (*Polysticta stelleri*) and spectacled eider. Since 2009, the U.S. Fish and Wildlife Service has been monitoring both species by ground pair surveys and aerial surveys (Graff 2016). This area supports a high diversity of nesting birds such as shorebirds, gulls and many waterfowl species such as lesser snow goose (*Chen caerulescens caerulescens*), greater white-fronted goose, black brant, cackling goose, tundra swan, king eider (*Somateria spectabilis*), and long-tailed duck (*Clangula heymalis*) (Amundson et al. 2019).

1.2.2 Field Methods

1.2.2.1 Kigigak Island

The USFWS delineated 48, 412 m × 412 m (0.17 km²) nest plots on Kigigak Island for monitoring (Moran 2000). USFWS personnel searched these nest plots for nesting spectacled eiders starting mid to late May when eiders typically initiate egg laying. Spectacled eider nests were located by systematically searching the plots with the aid of aerial photo maps, GPS units to reference plot boundaries, and binoculars. After flushing the hen from the nest, the observer recorded nest information, including nest coordinates and the number of eggs in the nest. Nests that were incidentally found outside of nest plot were still recorded and included in the sample.

1.2.2.2 Utqiagvik

In 1999, the USFWS established a study area that aimed to find Steller's eider nests in the vicinity of Utqiagvik (Obritschkewitsch et al. 2001) and in 2009 implemented spectacled

eider nest monitoring (Safine 2011). The study area is approximately 170 km² and within about 6 km of the road system. This area is divided into 26 sub-areas of varying sizes which are separated by land features such as streams, lakes, roads, or any land mark that can easily be referenced to avoid the possibility of overlapping search areas. Due to the vastness of the study area and low density of targeted nesting birds, ground-based surveys were conducted first and were intended to cover 100% of the study area. The aim of the ground-based surveys was to locate potential nesting areas for Steller's and spectacled eiders. Nest searching began in early June, after the ground-based surveys, which is typically when enough snow cover has melted for the eiders to initiate egg laying. Each observer used binoculars to help aid in detection of cryptic nesting birds. Observers used handheld GPS/data collection devices (Juno SB, Trimble Navigation Limited, Colorado, USA) to record the nest information.

At both sites, the extent of embryo development was assessed using egg floatation (Westerskov 1950) and egg candling (Hanson 1954) to predict the hatching date of the clutch. We checked the status of some nests prior to their predicted hatch date. The final fate of each nest (hatched vs. failed) was determined by revisiting the nest after the projected hatch date; the presence of egg membranes in the nest indicated hatched eggs. A nest was deemed successful if at least one egg membrane was present in the nest. A nest was considered failed if the entire clutch was damaged by the predators, missing prior to its hatching date, or cold and unattended, indicating abandonment.

1.2.3 Data Analyses

We examined the effects of conditions during the winter in each of the three breeding response variables: 1) nest initiation date, 2) clutch size, 3) nest survival.

1.2.3.1 Nest Initiation Date

In our analysis of nest initiation date, we included all nests that were monitored from the time they were discovered until they either hatched or failed. Initiation date was estimated based on extent of embryo development of the first egg laid as determined by candling or floating eggs. We analyzed variation in the Julian date of nest initiation using general linear mixed effects models using the packages ‘lme4’, ‘merTools’, and ‘plotrix’ in program R (Lemon 2006, Bates et al. 2015, Knowles and Fredrick 2020, R Core Team 2022). We included a random effect of year to account for the interannual variation unrelated to annual winter and weather variables (Bates et al. 2015).

1.2.3.2 Clutch Size

For analysis of clutch size, we only included nests that had reached their complete clutch size and started the incubation process so the sample was not biased by any incomplete clutches. Using this approach, we excluded nests that were discovered during laying and had their next observation status of either unknown, abandoned, or predated. We analyzed variation in clutch size using Poisson log-linear models to examine sources of variation in the count of eggs in nests. Poisson log-linear models are generalized linear models that assume a Poisson distribution and use a log link to the data. To achieve model convergence, we standardized winter ice days and ice index explanatory variables. To run our models, we used program R (R Core Team 2022) and used the statistical packages ‘lme4’ and ‘plotrix’ to run models and included a random effect on year (Lemon 2006, Bates et al. 2015).

1.2.3.3 Nest Survival

We included nests that were monitored from discovery until their final status was determined with certainty to be either success or failure. For successful nests, we assumed a 24-

day incubation period (Flint and Grand 1999). If nests were found after the egg laying period, we backdated 24 days from hatch to calculate the nest initiation date. However, if a nest contained all inviable eggs and the hen incubated for 24 days, it was considered a successful nest for the purpose of calculating nest survival because the hen incubated the eggs for the duration that would allow viable eggs to hatch. Nests that had no final fate or insufficient data to determine the final nest fate were not included in the analysis.

We estimated daily survival rate (DSR) of spectacled eider nests using the nest survival analysis module in Program MARK (Dinsmore et al. 2002, Rotella et al. 2004) implemented through the ‘RMark’ package (Laake 2013) in Program R (R Core Team 2022). Nest survival models are generalized linear models that assume a binomial distribution and use a logit link to the data. We analyzed data from Kigigak Island and Utqiagvik study areas together using a site categorical variable to test for differences between sites, because we assumed the estimates would be different between two sites given they are separated by > 10 degrees latitude.

1.2.3.4 Candidate Models

In our analyses of breeding response variables, we considered previous hypotheses related to winter conditions supported by analyses of spectacled eider apparent survival (Flint et al. 2016, Christie et al. 2018), breeding abundance (Petersen and Douglas 2004), and the apparent nest success component of integrated population models (Dunham et al. 2021). We examined variables supported in models of annual survival and abundance (Table 1) based on the hypothesis that factors that were associated with decreased survival and abundance may also have sublethal effects expressed during the breeding season. Therefore, we used the same model structure with the same explanatory variables to model variation in our response variables (Table 2).

We quantified winter sea ice cover using the approach used in previous studies that was based on the core wintering area identified by Peterson and Douglas (2004) using locations from spectacled eiders carrying satellite transmitters from 1993 to 1997. This area is encompassed by four 25×25 km grid cells in the Bering Sea, south of St. Lawrence Island (Petersen and Douglas 2004). Satellite transmitters deployed more recently indicate spectacled eiders consistently winter south of St. Lawrence Island, but the core area varies annually (Cooper et al. 2013, Sexson et al. 2014). The core area delineated by Peterson and Douglas (2004), however, has been used to consistently index sea ice concentrations in the broader Bering Sea wintering area (Flint et al. 2016, Christie et al. 2018, Dunham et al. 2021).

Sea ice concentration data on the core area were derived from satellite imagery created using passive microwave radar (Comiso 2017). We obtained bootstrap sea ice concentration estimates from the National Snow and Ice Data Center (NSIDC). To represent daily sea ice concentration in the core area, we followed the previously used method by Peterson and Douglas (2004) that selects the minimum percent sea ice concentration value among the four squares for each day of winter (01 November – 31 March) to create the winter ice variable (Petersen and Douglas 2004, Flint et al. 2016, Christie et al. 2018).

Flint et al. (2016) used sea ice concentration data in the core area to create an index of ice severity in the Bering Sea wintering area. The index of ice severity (*ice index*) takes into account runs of consecutive days of high ($\geq 95\%$) ice cover, allowing for 1-day breaks

$$I = \sum_{i=1}^B D \times \ln(D)$$

where B is the total number of consecutive day periods that meet the 95% ice cover within a year and D is the number of days in each period. Following Flint et al. (2016), we calculated the extreme ice index for each winter (November – April). This equation emphasizes consecutive

days with sea ice cover $\geq 95\%$ ice cover, where years with more lengthy periods of ice cover will have a greater index. A higher index indicates more extreme ice conditions and a lower index indicates milder ice conditions.

Following Peterson and Douglas (2004), we obtained spring temperature and wind data during April of each year from the weather station at St. Paul Island airport, which is the weather station nearest to the spectacled eider wintering area (National Climate Data Center Station CHCND:USW00025713). To summarize daily ambient temperature, we calculated extreme temperature days for spring as the number of days with a minimum daily temperature $\leq 5^{\text{th}}$ percentile (-11.1°C) of the data between 1994 – 2021 (*spring extreme temperature*). Similarly, we calculated extreme wind speed days for spring, as the number of days with maximum wind speeds $\geq 95^{\text{th}}$ percentile (13.6 km/hr) over the same period of years (*spring extreme wind*).

We used these explanatory variables in model structures previously supported in studies (Petersen and Douglas 2004, Flint et al. 2016, Christie et al. 2018, Dunham et al. 2021; Table 2). We also included 2 additional models, the first with winter ice as a quadratic effect additive to the effects of spring temperature and spring wind and the second with winter ice as a linear effect.

We used these 5 models in candidate model sets for both nest initiation date and clutch size with the addition of an additive site effect under the hypothesis that the potential effects of winter conditions would be in the same direction (either positive or negative) at both Kigigak Island and Utqiagvik. In our analysis of nest survival, we first examined the effects of nest age, nest initiation date, year, and site. We then included the variables that were supported in that analysis to each of the 5 candidate winter effects models. In each candidate model set, we also included a null model that held the response variable constant as a measure of model fit.

To assess the amount of support for each model given the data relative to all the models we considered, we used Akaike's Information Criterion adjusted for small sample size (AIC_c) (Burnham and Anderson 2002). Models with more support from the data have lower AIC_c values. We calculated AIC_c statistics, including AIC_c differences (ΔAIC_c), the difference in AIC_c values between the most supported model with the lowest AIC_c value and each model in the candidate model set, and AIC_c model weights, which are bound between 0 and 1 within a model set with higher values indicating more support for a model (Burnham and Anderson 2002). We based inference on parameter estimates and 95% confidence intervals from models with $\Delta AIC_c < 2$.

1.3 Results

1.3.1 Nest Initiation Date

We examined the variation in mean nest initiation date using 2,780 ($n_{\text{Kigigak Island}} = 2,705$, $n_{\text{Utqiagvik}} = 165$) spectacled eider nests in Alaska from 1994 – 2019 and 2021 (Table 3). Across this sample of nests, nest initiation date ranged from 07 May to 26 June at Kigigak Island, and 30 May to 06 July at Utqiagvik. Of the six models in the candidate set, the model containing winter ice days and site was most supported model by the data (weight = 0.45) (Table 4). Mean nest initiation date differed by 20 days between sites, with Kigigak Island having consistently earlier nest initiation dates than Utqiagvik. The overall mean Julian nest initiation date for Kigigak Island was Julian day 149 (29 May) (95% CI: 148.62, 149.18) and Utqiagvik was Julian day 169 (16 June) (95% CI: 168.41, 170.36) (Fig 1). Initiation date showed a weak positive relationship with winter ice days ($\beta_{\text{winter ice}} = 0.03$, 95% CI: -0.06, 0.12), suggesting that nest initiation occurred later following more ice cover on the wintering area, but this effect was small, only 2 days.

1.3.2 Clutch Size

In the analysis of clutch size, we used 2,932 spectacled eider nests ($n_{\text{Kigigak Island}} = 2,763$, $n_{\text{Utqiagvik}} = 169$). Of the six models we considered, the null model had all the support indicating that preceding winter ice and spring weather conditions were not associated with variation in clutch size (weight = 1.0) (Table 5). However, we found very little variation in clutch size within or between sites. The mean clutch size for nests at Kigigak Island was 4.8 (95% CI: 4.7, 4.8), and Utqiagvik had a mean clutch size of 4.3 (95% CI: 4.1, 4.5), which the confidence intervals for both sites indicate little variation.

1.3.3 Nest Survival

We monitored the fates of 2,870 spectacled eider nests in Alaska from 1994 – 2019 and 2021 ($n_{\text{Kigigak Island}} = 2,705$, $n_{\text{Utqiagvik}} = 165$) (Table 3). Nest monitoring data from Kigigak Island included 1994 – 2015, 2019, and 2021 and Utqiagvik 2010 – 2019.

In the first stage of modeling of nest survival, we considered models that included covariates that may confound our understanding of how winter conditions affected nest survival. This best supported model (weight = 0.42) from the preliminary stage of the analysis included a site-year interaction term and additive effects of nest age and nest initiation date (Table 6). Initiation date and nest age were negatively associated with daily survival rate (DSR) ($\beta_{\text{init}} = -0.046$, 95% CI: -0.062, -0.032; $\beta_{\text{nest age}} = -0.016$, 95% CI: -0.031, -0.002). Nest survival, the probability that at least 1 egg will survive a 24-day incubation period, varied between years. For Kigigak Island the lowest nest survival was 0.11 (95% CI: -0.02, 0.24) in 2001 and the highest nest survival was 0.95 (95% CI: 0.92, 0.98) in 2007, and at Utqiagvik the lowest nest survival was 0.40 (95% CI: 0.16, 0.63) in 2016 and the highest nest survival was 0.83 (95% CI: 0.66,

0.99) in 2018. The overall mean nest survival at Kigigak Island and Utqiagvik was 0.78 (95% CI: 0.71, 0.86) and 0.67 (95% CI: 0.58, 0.76), respectively (Fig 2).

In the second stage of model fitting, the model most supported by the data included spring extreme temperature, spring extreme wind, winter ice as a quadratic trend, nest initiation date, nest age, and site (weight = 0.90) (Table 7). Spring extreme temperatures and spring extreme winds were negatively associated with DSR ($\beta_{\text{temp}} = -0.080$, 95% CI: -0.125, -0.035 and $\beta_{\text{wind}} = -0.117$, 95% CI: -0.183, -0.051) (Fig 3, 4). Nest DSR was negatively associated with nest initiation date ($\beta_{\text{init}} = -0.045$, 95% CI: -0.578, -0.033) (Fig 5). However, in this top model the confidence intervals for the nest age parameter broadly overlapped zero ($\beta_{\text{nest age}} = 0.0001$, 95% CI: -0.010, 0.014), indicating that after accounting for variation in daily nest survival related to winter and ice, the effect of nest age was no longer important.

Nest survival at Kigigak Island decreased from 0.72 (95% CI: 0.66, 0.78) at zero spring extreme temperature days to 0.61 (95% CI: 0.37, 0.79) at seven spring extreme temperature days. Nest survival at Utqiagvik showed a similar pattern, at zero spring extreme temperature days nest survival was 0.85 (95% CI: 0.77, 0.90) and decreased to 0.78 (95% CI: 0.58, 0.90) at seven spring extreme temperature days. For spring extreme wind days, nest survival at Kigigak Island decreased from 0.73 (95% CI: 0.37, 0.80) at zero days of spring extreme winds to 0.62 (95% CI: 0.37, 0.80) at five days of spring extreme winds. Utqiagvik showed a similar pattern. Nest survival decreased from 0.86 (95% CI: 0.78, 0.91) at zero days of spring extreme winds to 0.79 (95% CI: 0.59, 0.90) at five days of spring extreme winds.

As a function of nest initiation, nest survival at Kigigak Island decreased from 0.87 (95% CI: 0.81, 0.91) for early initiated nests (initiation date = 08 May) to 0.34 (95% CI: 0.08, 0.63) for late initiated nests (initiation date = 26 June). For Utqiagvik, nest survival decreased from 0.83

(95% CI: 0.75, 0.89) for early initiated nests (nest initiation date = 30 May) to 0.43 (95% CI: 0.14, 0.70) for late initiated nests (nest initiation date = 06 July).

Winter ice days were negatively associated with DSR ($\beta_{\text{winter ice}} = -0.0002$, 95% CI: -0.00035, -0.000045) (Fig 6). Across the range of winter ice days, nest survival at Kigigak Island increased from 0.41 (95% CI: 0.26, 0.55) at zero winter ice days to 0.65 (95% CI: 0.48, 0.78) at 62 winter ice days, and remained at a similar value 0.64 (95% CI: 0.37, 0.82) at the maximal value of 79 winter ice days. Nest survival at Utqiagvik showed a similar pattern, but was consistently higher than Kigigak island. At zero winter ice days, nest survival at Utqiagvik was 0.64 (95% CI: 0.47, 0.77) and increased to 0.81 (95% CI: 0.66, 0.90) at 62 winter ice days and remained high 0.80 (95% CI: 0.58, 0.91) at the maximal value of 79 winter ice days.

1.4 Discussion

We investigated how winter ice and spring weather conditions in the Bering Sea were associated with the reproductive performance of spectacled eiders during the subsequent breeding season. We found temporal and spatial variation in nest initiation, nest survival, and little spatial or temporal variation in clutch size. At both sites, mean nest initiation date showed a trend of occurring slightly later following winters with high ice cover in the Bering Sea, although the effect size was small indicating nest initiation is not really influenced by preceding winter ice conditions. Nest survival differed across years and was lowest when winter ice days were low and increased to an asymptote with increasing number of winter ice days. Both sites showed this pattern, but nest DSR was consistently higher at Utqiagvik than at Kigigak Island after accounting for winter ice days. Spring extreme temperature and wind conditions had negative associations with nest survival. Nest survival decreased as the count of days of spring extreme winds and temperatures increased. In contrast, we found no relationship between clutch size and

ice or weather variables. Overall, we found evidence that winter conditions in the Bering Sea were associated with nest survival, but not nest initiation date or clutch size in spectacled eiders.

The timing of nest initiation at Kigigak Island and Utqiagvik differed by about 20 days with eiders nesting earlier at Kigigak Island. This was likely related to the later onset of spring in the Arctic compared to sub-Arctic. At both sites, winter high ice days showed a weak positive relationship with nest initiation date. Nest initiation date increased by only 2 days across the range of high ice days. Spectacled eiders that nest on the YKD and ACP depart from the Bering Sea at the same time (Sexson et al. 2014). Due to the later snowmelt in the ACP the eiders stage in coastal areas along the Chukchi and Beaufort seas until they are able to start nesting. Thus, eiders breeding on the ACP have an additional 20 days before initiating nests than eiders breeding at Kigigak Island.

We found no evidence of cross-seasonal effects on nest initiation. However, other environmental factors may explain variation in nest initiation we found within sites. Grand and Flint (1997) showed that late snowmelt and river ice break-up during the spring on the YKD were associated with later nest initiation by spectacled eiders. Chaulk and Mahoney (2012) found that common eiders at sub-Arctic breeding areas in Canada delayed nest initiation when there was extensive ice cover during the spring before the laying period. Love et al. (2010) also found nest initiation date in common eiders was earlier when spring temperatures were warmer. Therefore, spring environmental conditions closer to the breeding area prior to the breeding season may better explain variation in nest initiation date than conditions at the wintering area.

We found no evidence of carry-over effects in the clutch size of spectacled eiders' nests at either Kigigak Island or Utqiagvik. Even across winters with very different ice conditions in the Bering Sea, mean clutch size showed little variation across years. We hypothesized that high-

ice winters in the Bering Sea increased eider energy costs by decreasing accessibility to benthic prey, which ultimately would be associated with poor spring body condition in eiders. Females in poorer body condition would, in turn, produce smaller clutches, as has been demonstrated in other species (Coulson 1999, Opper et al. 2010). However, our data showed very little variation in clutch size across years suggesting conditions prior to the breeding season had no effect on clutch size.

We predicted the variation in nest DSR would be explained by ice conditions prior to their breeding season. There is evidence that winter conditions in the Bering Sea impact adult female survival (Petersen and Douglas 2004, Flint et al. 2016, Christie et al. 2018). Christie et al. (2018) found a non-linear relationship between sea ice and adult survival, where apparent survival estimates tended to be lower following winters with few or many days with winter ice days and apparent survival was highest when there was a moderate number of high winter ice days. In our analysis of nest survival, we observed a similar but not identical pattern, with ice in a data set with more low ice years. Nest DSR was lowest when the count of winter high ice days was at the minimum and increased with the count of winter high ice days. We found no evidence that DSR declined following high ice winters, but rather remained high. Nest DSR when days of winter ice were at the maximum were similar to the estimates when count of days were around the 45 – 65 range. In our results, nest DSR estimates from Utqiagvik were consistently higher than estimates from Kigigak Island across the range of winter ice days only after winter ice was included in the model. One possible explanation is the difference in nest initiation between Kigigak Island and Utqiagvik which gives eiders at Utqiagvik more time to recover from poor winter conditions. Eiders breeding at Kigigak Island initiate nests shortly after departing the wintering area, in contrast spectacled eiders breeding at Utqiagvik depart the wintering area at

the same time, but spend an additional 20 days along the coast of the Chukchi and Beaufort seas before they can initiate nests. If foraging conditions are good at those coastal staging areas, eiders may be able to increase their body condition prior to breeding.

Nutrient acquisition strategy may underlie our mixed results, where winter conditions were associated with nest survival, but not nest initiation date or clutch size. At Utqiagvik, stable isotope ratios in the egg membranes from hatched eggs indicated nutrients used to produce eggs were from freshwater food resources on the breeding area, while the stable isotope ratios from the red blood cells of incubating eiders were from marine resources in non-breeding habitat (Miller et al. 2022). This result indicates that egg production in spectacled eiders is not associated with winter ice conditions from the Bering Sea. If female spectacled eiders breeding at Kigigak Island use the same nutrient allocation strategy, breeding area conditions would be more important to clutch size than wintering area conditions, which may explain the lack of relationship between ice conditions and clutch size. Further, we found very little variation in mean clutch size, suggesting that variation in clutch size may be buffered by breeding propensity. Our sample only included birds that initiated nests and those that did not breed may not have reached threshold body condition required to produce a full clutch and therefore did not breed. Once a female decides to breed, clutch size may be relatively fixed. King eiders, a similar species, use an income breeding strategy where they rely on nutrients from breeding areas to produce their clutches (Oppel et al. 2010). Comparing it to a smaller species harlequin ducks (*Histrionicus histrionicus*) allocate mostly freshwater nutrients to develop their eggs during reproduction (Bond et al. 2007). Coulson (2010) found female common eiders, a known capital breeder that builds up body weight prior to breeding to use for egg production, will decide to nest if they have acquired adequate reserves. If feeding conditions are poor, common eiders forgo

breeding (Coulson 1984). The lack of variation in the clutch size of spectacled eiders may be due to some combination of high food availability at the breeding area and deferred breeding by eiders in poor body condition.

Spectacled eider's use of marine derived nutrients for incubation may be the mechanism linking wintering conditions on the Bering Sea with nest survival. The same mechanism hypothesized to potentially cause decreased survival in spectacled eiders may also reduce body condition. At the Bering Sea south of St. Lawrence Island, spectacled eiders forage on benthic prey by diving (Petersen et al. 1998). Arctic sea ice extent has declined since 1979 (Barber et al. 2017, Comiso et al. 2017), and in the past decade there have been years with extremely low ice cover in the Bering Sea (Stabeno and Bell 2019, Danielson et al. 2020). Spectacled eiders wintering at the Bering Sea need open water to forage and sea ice to dampen the wave action and to use for roosting (Lovvorn et al. 2009, 2014). Also, low ice cover events indicate that the winter in the Arctic and sub-Arctic are becoming milder and warmer, and the warming trend may lead to shifts in distribution of benthic forage species (Grebmeier et al. 2006, Lovvorn et al. 2009, Grebmeier 2012, Goethel et al. 2019). Additionally, it has been shown in common eiders that brood abandonment is more likely when female body condition is poor (Bustnes et al. 2002). Thus, the declining sea ice along with the reduction of benthic prey can result in poor female body condition, which can reduce incubation constancy in the following breeding season to lower nest survival and increase chance of brood abandonment.

The viability of the spectacled eider population in the future likely depends on ice conditions in the Bering Sea. Sea ice concentration at the core wintering area of the spectacled eiders projected under various climate change scenarios showed an initial population increase during the period of moderate sea ice conditions, followed by decline when sea ice conditions

became consistently low (Christie et al. 2018). This predicted decline was based only on the association between ice and adult survival. In our study, we found evidence that low ice conditions were also associated with low productivity through reduced nest survival. If low ice conditions reduce both adult survival and productivity, future population declines under low ice conditions may be even more rapid than predicted.

1.4.1 Summary and Future Work

Climate change is affecting sea ice in the Bering Sea, and consequently, multiple vital rates of spectacled eiders. This study provides insights on the effects of winter ice conditions and spring extreme temperature and spring extreme wind conditions on the reproductive performance of breeding spectacled eiders in Alaska. We found no evidence that nest initiation date and clutch size components of productivity were influenced by winter ice conditions, but rather may be more related to conditions at the breeding area. We have found moderate to high ice conditions in the Bering Sea are favorable to the breeding success of spectacled eiders through increased nest survival. These results are similar to Christie et al. (2018), who found apparent survival of adult female spectacled eiders was highest following years of moderate high ice days in the Bering Sea. We also found low counts of winter ice days resulted in lower nest survival, which may be related to energetic costs prior to the breeding season. From 2015 – 2021 there were 4 years when the Bering Sea had less than 20 days with 95% or more ice cover at the wintering area of spectacled eiders. Prior to 2015, every winter back to at least 1993 had 25 or more winter ice days. With further loss of sea ice in the Bering Sea likely to continue to occur due to climate change, it is important to know how the spectacled eider will respond to inform Endangered Species Act listing and management decisions.

In addition, it is unknown whether the core wintering area of spectacled eiders will shift in response to sea ice loss. Future work should consider if spectacled eiders shift their core wintering area because if they do, the current core wintering area used to index winter conditions may no longer be relevant. Further, body condition of female spectacled eiders is critical to reproductive success. Winter food availability may influence breeding propensity (Coulson 2010), incubation constancy during nesting (Schmutz et al. 2006, Miller et al. 2022), and brood rearing post hatch (Bustnes et al. 2002). Measuring the body condition of females at spring arrival to the breeding area across years with differing ice conditions, may provide some insight into the importance of body condition as a mechanism influencing breeding performance.

1.5 Literature cited

- Amundson, C. L., P. L. Flint, R. A. Stehn, R. M. Platte, H. M. Wilson, W. W. Larned, and J. B. Fischer (2019). Spatio-temporal population change of arctic-breeding waterbirds on the Arctic Coastal Plain of Alaska. *Avian Conservation and Ecology* 14.
- Barber, D. G., W. N. Meier, S. Gerland, C. J. Mundy, M. Holland, S. Kern, L. Zhijun, C. Michel, D. K. Perovich, and T. Tamura (2017). Snow, water, ice and permafrost in the Arctic summary (SWIPA). Oslo:103–136.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bond, J. C., D. Esler, and K. A. Hobson (2007). Isotopic evidence for sources of nutrients allocated to clutch formation by harlequin ducks. *The Condor* 109:698–704.
- Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York. 2nd edition.
- Bustnes, J. O., Kjell E, Bjørn, and Tor H (2002). Body condition and brood abandonment in common eiders breeding in the high Arctic. *Waterbirds* 25:63–66.
- Chaulk, K. G., and M. L. Mahoney (2012). Does spring ice cover influence nest initiation date and clutch size in common eiders? *Polar Biology* 35:645–653.
- Christie, K. S., T. E. Hollmen, P. Flint, and D. Douglas (2018). Non-linear effect of sea ice: spectacled eider survival declines at both extremes of the ice spectrum. *Ecology and Evolution* 8:11808–11818.
- Comiso, J. C. (2017). Bootstrap sea ice concentration from Nimbus-7 SMMR and DMSP SSM/I-SSMIS, Version 3. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center.

- Comiso, J. C., W. N. Meier, and R. Gersten (2017). Variability and trends in the Arctic Sea ice cover: Results from different techniques. *Journal of Geophysical Research: Oceans* 122:6883–6900.
- Cooper, L. W., M. G. Sexson, J. M. Grebmeier, R. Gradinger, C. W. Mordy, and J. R. Lovvorn (2013). Linkages between sea-ice coverage, pelagic-benthic coupling, and the distribution of spectacled eiders: Observations in March 2008, 2009 and 2010, northern Bering Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography* 94:31–43.
- Coulson, J. C. (1984). The population dynamics of the Eider Duck (*Somateria mollissima*) and evidence of extensive non-breeding by adult ducks. *Ibis* 126:525–543.
- Coulson, J. C. (1999). Variation in clutch size of the common eider: A study based on 41 breeding seasons on Coquet Island, Northumberland, England. *Waterbirds: The International Journal of Waterbird Biology* 22:225–238.
- Coulson, J. C. (2010). A long-term study of the population dynamics of common eiders (*Somateria mollissima*): Why do several parameters fluctuate markedly? *Bird Study* 57:1–18.
- Danielson, S. L., O. Ahkinga, C. Ashjian, E. Basyuk, L. W. Cooper, L. Eisner, E. Farley, K. B. Iken, J. M. Grebmeier, L. Juranek, G. Khen, et al. (2020). Manifestation and consequences of warming and altered heat fluxes over the Bering and Chukchi Sea continental shelves. *Deep-Sea Research Part II: Topical Studies in Oceanography* 177:104781.
- Dau, C. P., and S. A. Kistchinski (1977). Seasonal movements and distribution of the spectacled eider. *Wildfowl* 28:65–75.
- Dinsmore, S. J., G. C. White, and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.

- Duffy-Anderson, J. T., P. Stabeno, A. G. Andrews, K. Cieciel, A. Deary, E. Farley, C. Fugate, C. Harpold, R. Heintz, D. Kimmel, K. Kuletz, et al. (2019). Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. *Geophysical Research Letters* 46:9833–9842.
- Dunham, K. D., A. M. Tucker, D. N. Koons, A. Abebe, F. S. Dobson, and J. B. Grand (2021). Demographic responses to climate change in a threatened Arctic species. *Ecology and Evolution* 11:10627–10643.
- Flint, P. L., and J. B. Grand (1999). Incubation period of spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. *The Condor* 101:413–416.
- Flint, P. L., J. B. Grand, J. A. Morse, and T. F. Fondell (2000). Late summer survival of adult female and juvenile spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. *The International Journal of Waterbird Biology* 23:292–297.
- Flint, P. L., J. B. Grand, and M. R. Petersen (2016). Effects of lead exposure, environmental conditions, and metapopulation processes on population dynamics of spectacled eiders. *North American Fauna* 81:1–41.
- Franson, J. C., M. R. Petersen, C. U. Meteyer, and M. R. Smith (1995). Lead poisoning of spectacled eiders (*Somateria fischeri*) and of a common eider (*Somateria mollissima*) in Alaska. *Journal of Wildlife Diseases* 31:268–271.
- Goethel, C. L., J. M. Grebmeier, and L. W. Cooper (2019). Changes in abundance and biomass of the bivalve *Macoma calcarea* in the northern Bering Sea and the southeastern Chukchi Sea from 1998 to 2014, tracked through dynamic factor analysis models. *Deep-Sea Research Part II: Topical Studies in Oceanography* 162:127–136.

- Graff, N. (2016). Breeding ecology of Steller's and spectacled eiders nesting near Barrow, Alaska 2015. U. S. Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office, Fairbanks, Alaska. Technical Report.
- Grand, J. B., and P. L. Flint (1997). Productivity of nesting spectacled eiders on the lower Kashunuk River, Alaska. *The Condor* 99:926–932.
- Grand, J. B., P. L. Flint, M. R. Petersen, and C. L. Moran (1998). Effect of lead poisoning on spectacled eider survival rates. *The Journal of Wildlife Management* 62:1103–1109.
- Grebmeier, J. M. (2012). Shifting patterns of life in the Pacific Arctic and sub-Arctic Seas. *Annual Review of Marine Science* 4:63–78.
- Grebmeier, J. M., J. E. Overland, S. E. Moore, E. V. Farley, E. C. Carmack, L. W. Cooper, K. E. Frey, J. H. Helle, F. A. McLaughlin, and S. L. Mcnutt (2006). A major ecosystem shift in the northern Bering Sea. *Science* 311:1461–1464.
- Hanson, C. H. (1954). Criteria of age of incubated mallard, wood duck, and Bob-white quail eggs. *The Auk* 71:267–272.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- Knowles, J. E., C. Fredrick (2020). merTools: Tools for analyzing mixed effect regression models. R package version 0.5.2. <https://CRAN.R-project.org/package=merTools>.
- Laake, J. L. (2013). RMark: An R interface for analysis of capture-recapture data with MARK.
- Lemon, J. (2006). Plotrix: A package in the red light district of R. *R-News* 6(4):8–12.
- Lewis, K. C., G. A. Zyvoloski, B. Travis, C. Wilson, and J. Rowland (2012). Drainage subsidence associated with Arctic permafrost degradation. *Journal of Geophysical Research: Earth Surface* 117:1–18.

- Love, O. P., H. G. Gilchrist, S. Descamps, C. A. D. Semeniuk, and J. Bêty (2010). Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia* 164:277–286.
- Lovvorn, J. R., E. M. Anderson, A. R. Rocha, W. W. Larned, J. M. Grebmeier, L. W. Cooper, J. M. Kolts, and C. A. North (2014). Variable wind, pack ice, and prey dispersion affect the long-term adequacy of protected areas for an Arctic sea duck. *Ecological Applications* 24:396–412.
- Lovvorn, J. R., J. M. Grebmeier, L. W. Cooper, J. K. Bump, and S. E. Richman (2009). Modeling marine protected areas for threatened eiders in a climatically changing Bering Sea. *Ecological Applications* 19:1596–1613.
- Marcogliese, D. J. (2008). The impact of climate change on the parasites and infectious diseases of aquatic animals. *OIE Revue Scientifique et Technique* 27:467–484.
- Miller, M. W. C., J. R. Lovvorn, N. R. Graff, and N. C. Stellrecht (2022). Use of marine vs. freshwater proteins for egg-laying and incubation by sea ducks breeding in Arctic tundra. *Ecosphere* 13:e4138.
- Moran, C. L. (2000). Spatial-temporal variation in reproduction and site fidelity of spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska.
- Mueter, F. J., and M. A. Litzow (2008). Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecological Applications* 18:309–320.
- Obritschkewitsch, T., P. D. Martin, and R. S. Suydam (2001). Breeding biology of Steller's eiders nesting near Barrow, Alaska, 1999-2000. Ecological Services Fairbanks, Alaska, U. S. Fish and Wildlife Service. Technical Report.

- Oppel, S., A. N. Powell, and D. M. O'Brien (2010). King eiders use an income strategy for egg production: A case study for incorporating individual dietary variation into nutrient allocation research. *Oecologia* 164:1–12.
- Petersen, M. R., and D. C. Douglas (2004). Winter ecology of spectacled eiders: Environmental characteristics and population change. *The Condor* 106:79–94.
- Petersen, M. R., W. W. Earned, and D. C. Douglas (1999). At-sea distribution of spectacled eiders: A 120-year-old mystery resolved. *The Auk* 116:1009–1020.
- Petersen, M. R., J. F. Piatt, and K. A. Trust (1998). Foods of spectacled eiders (*Somateria fischeri*) in the Bering Sea, Alaska. *Wildfowl* 49:124–128.
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Raquel, A. J., J. H. Devries, D. W. Howerter, and R. G. Clark (2019). Reproductive consequences of climate variability in migratory birds: evidence for species-specific responses to spring phenology and cross-seasonal effects. *Oecologia* 191:217–229.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer (2004). Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:187–205.
- Safine, D. (2011). Breeding ecology of Steller's and spectacled eiders nesting near Barrow, Alaska 2008-2010. U.S. Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office, Fairbanks, Alaska. Technical Report.
- Scavia, D., J. C. Field, D. F. Boesch, R. W. Buddemeier, and V. Burkett (2002). Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* 25:149–164.

- Schamber, J. L., J. S. Sedinger, and D. H. Ward (2012). Carry-over effects of winter location contribute to variation in timing of nest initiation and clutch size in black brant (*Branta bernicla nigricans*). *The Auk* 129:205–210.
- Schmutz, J. A., K. A. Hobson, and J. A. Morse (2006). An isotopic assessment of protein from diet and endogenous stores: effects on egg production and incubation behaviour of geese. *Ardea* 94:385–397.
- Sedinger, J. S., and R. T. Alisauskas (2014). Cross-seasonal effects and the dynamics of waterfowl populations. *Wildfowl*:277–304.
- Sexson, M. G., J. M. Pearce, and M. R. Petersen (2014). Spatiotemporal distribution and migratory patterns of spectacled eiders. BOEM 2014-665. Bureau of Ocean Energy Management, Alaska Outer Continental Shelf Region, Anchorage, Alaska.
- Sexson, M. G., M. R. Petersen, G. A. Breed, and A. N. Powell (2016). Shifts in the distribution of molting spectacled eiders (*Somateria fischeri*) indicate ecosystem change in the Arctic. *The Condor* 118:463–476.
- Stabeno, P. J., and S. W. Bell (2019). Extreme conditions in the Bering Sea (2017–2018): Record-breaking low sea-ice extent. *Geophysical Research Letters* 46:8952–8959.
- Stehn, R. A., C. P. Dau, B. Conant, and W. I. Butler (1993). Decline of spectacled eiders nesting in western Alaska. *Arctic* 46:264–277.
- Terenzi, J., M. T. Jorgenson, and C. R. Ely (2014). Storm-surge flooding on the Yukon-Kuskokwim Delta, Alaska. *Arctic* 67:360–374.
- USFWS (1993). Final rule to list spectacled eider as threatened. *Federal Register* 58:27474–27480.

Westerskov, K. (1950). Methods for determining the age of game bird eggs. *The Journal of Wildlife Management* 14:56–67.

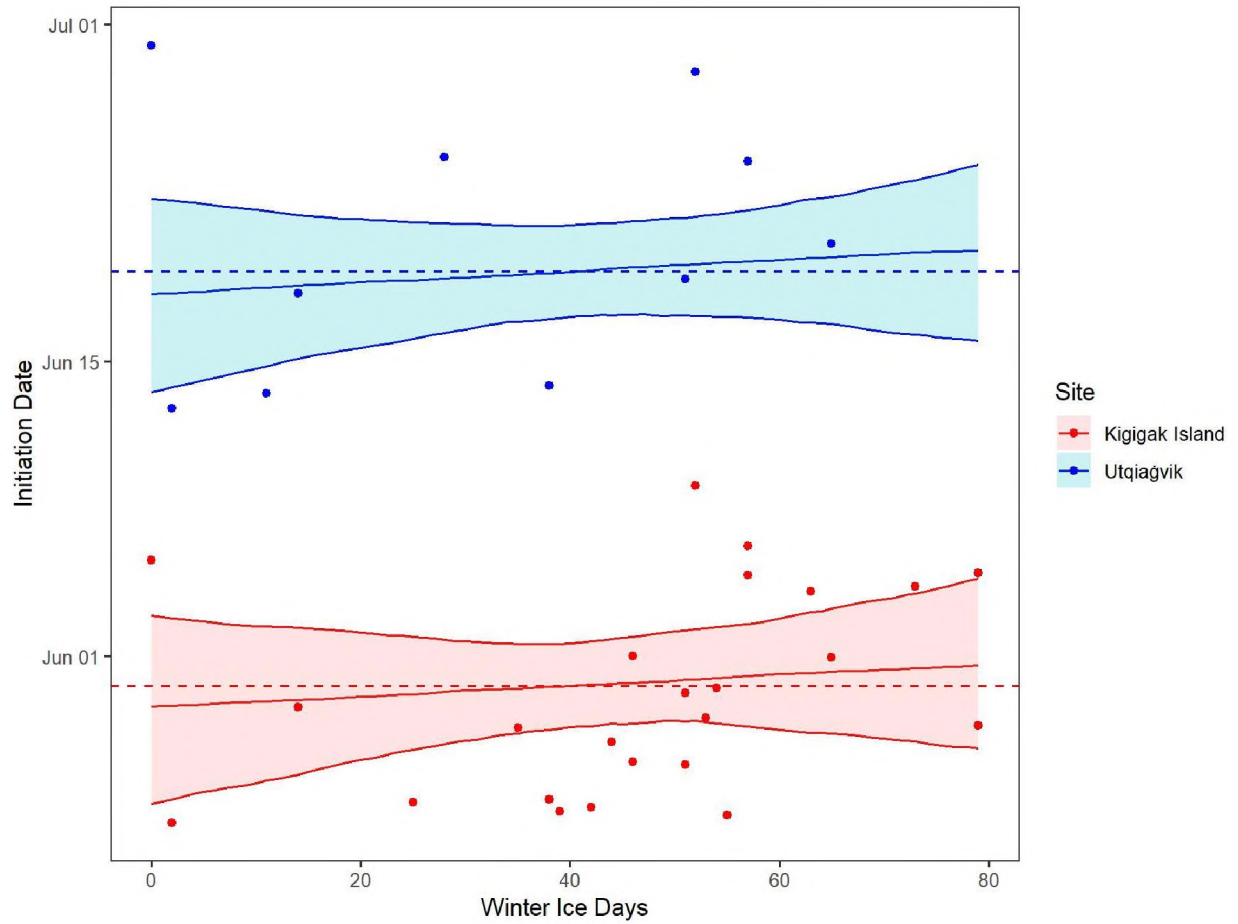


Figure 1. Annual mean nest initiation dates in relation to the number of winter ice days in the Bering Sea during winter for spectacled eiders nesting on Kigigak Island (red) and Utqiagvik (blue). The lines represent the fitted values for each site, with shaded areas representing the 95% confidence intervals. The dashed lines represent the overall mean nest initiation date.

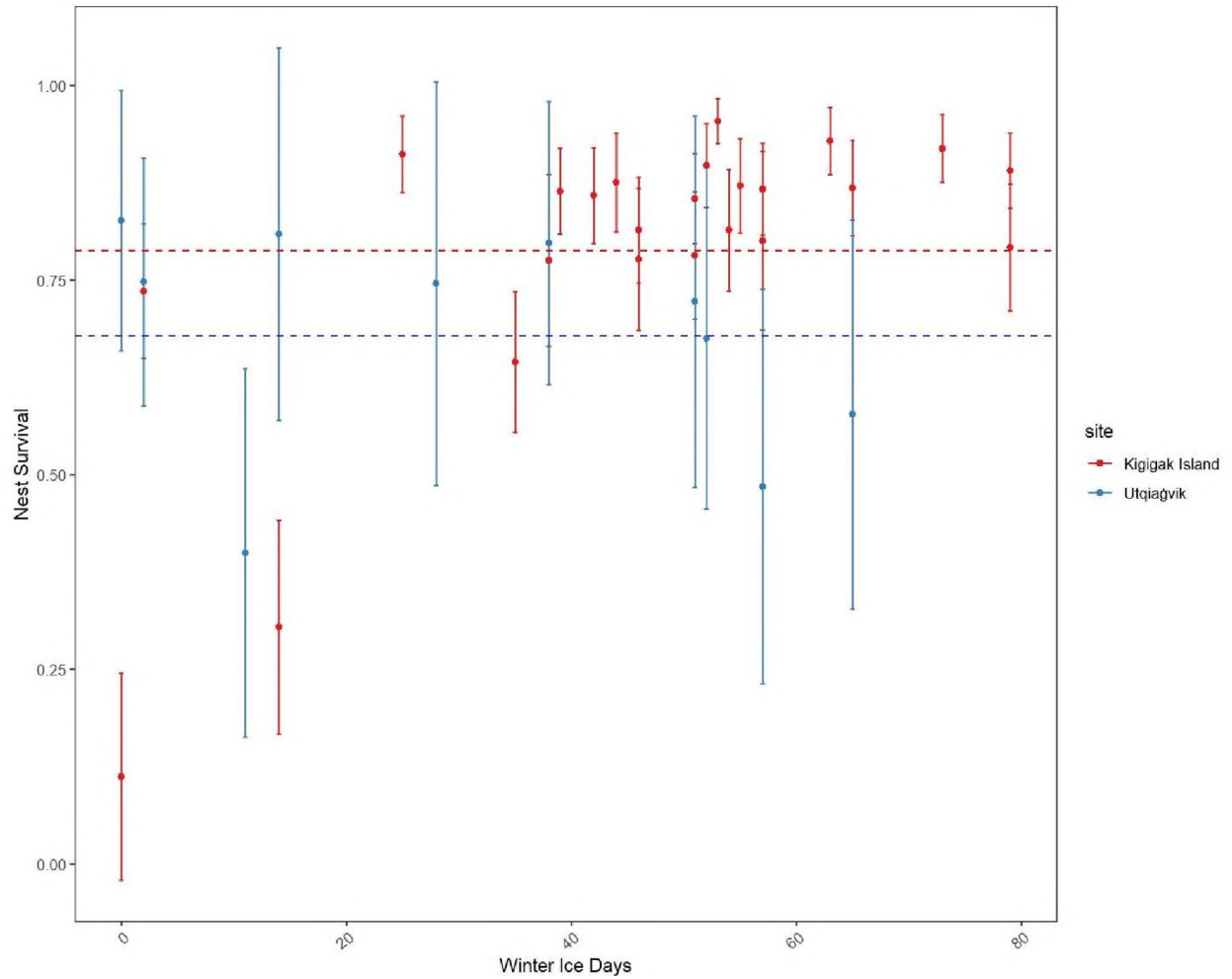


Figure 2. Annual nest survival probabilities as a function of winter ice days from the Bering Sea for spectacled eiders breeding at Kigigak Island (red) and Utqiagvik (blue), with vertical lines representing 95% confidence intervals. The dashed lines represent the mean nest survival for each site across all years.

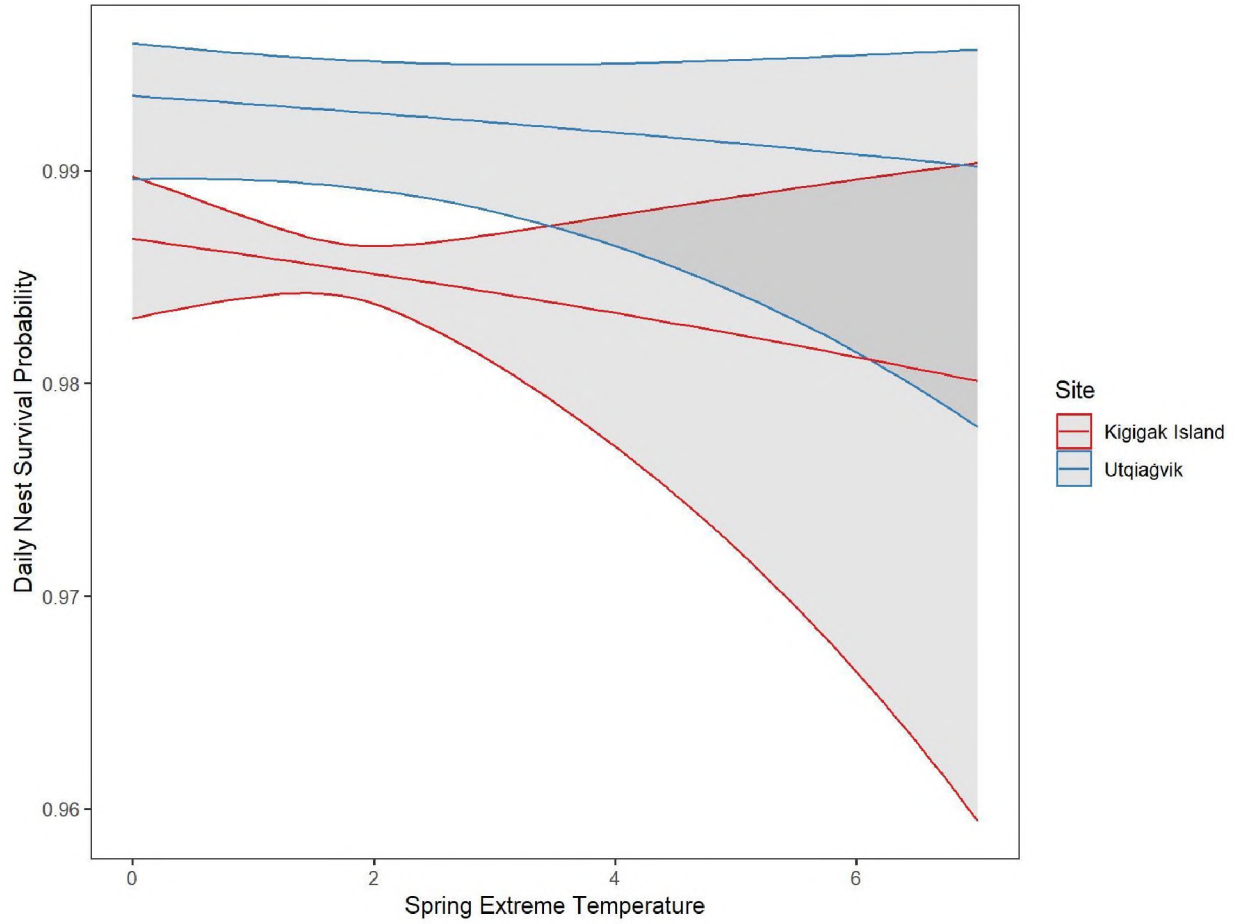


Figure 3. Nest daily survival rate (DSR) of breeding spectacled eiders on Kigigak Island (red) and Utqiagvik (blue) as a function of spring extreme temperature with shaded areas representing 95% confidence intervals.

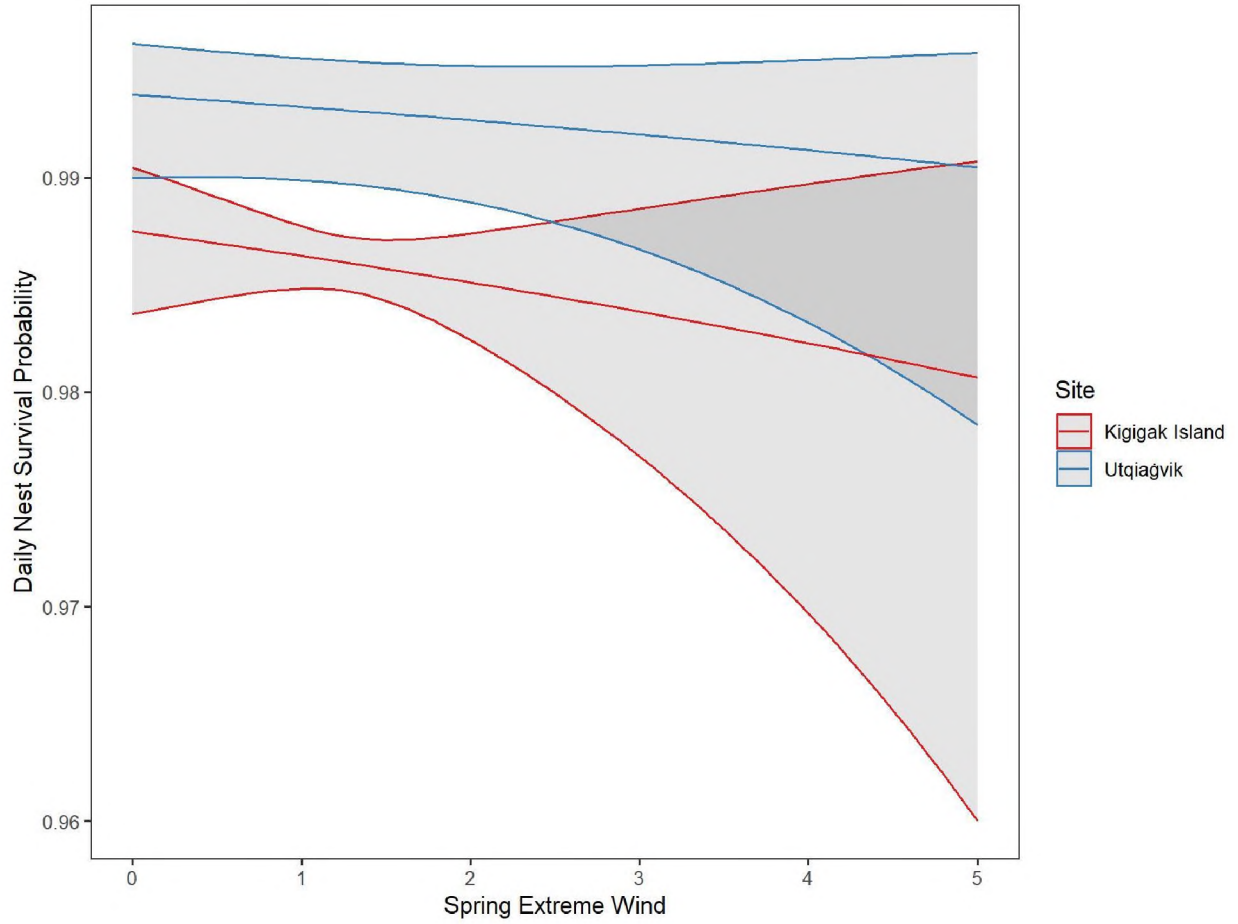


Figure 4. Nest daily survival rate (DSR) of breeding spectacled eiders on Kigigak Island (red) and Utqiagvik (blue) as a function of spring extreme wind with shaded areas representing the 95% confidence intervals.

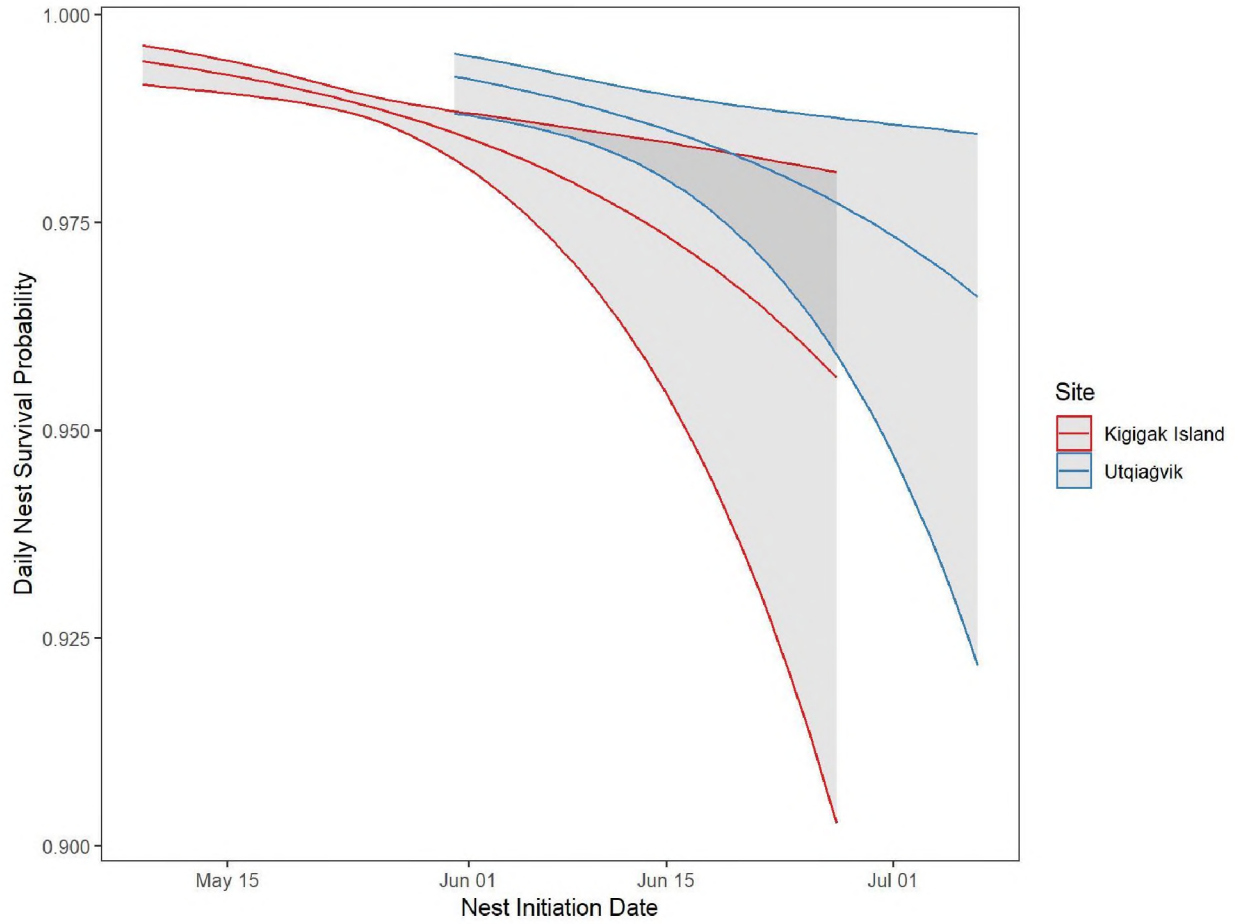


Figure 5. Nest daily survival rate (DSR) of breeding spectacled eiders on Kigigak Island (red) and Utqiagvik (blue) as a function of nest initiation date with shaded areas representing the 95% confidence intervals.

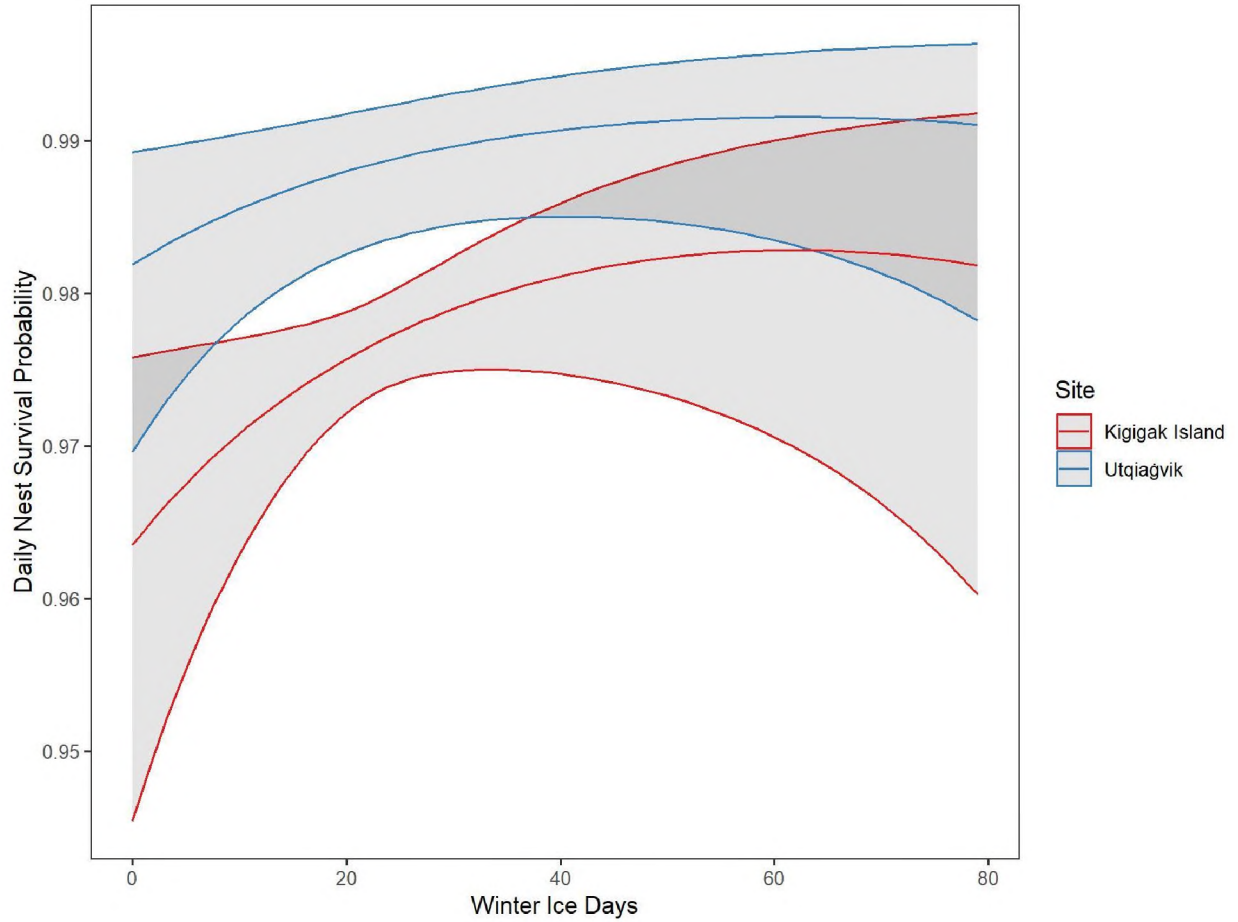


Figure 6. Nest daily survival rate (DSR) of breeding spectacled eiders on Kigigak Island (red) and Utqiagvik (blue) as a function of winter ice days from the Bering Sea with shaded areas representing the 95% confidence intervals.

Table.1 Explanatory variables used in models accounting for variation in nest initiation, clutch size, and nest survival.

| Parameter | Description | Analysis |
|----------------------------|---|--------------|
| Winter ice | Count of days with $\geq 95\%$ ice cover during winter season (November – March) | All analyses |
| Ice index | Ice severity index for long periods of ice cover with $\geq 95\%$ during winter and spring (November – April) | All analyses |
| Spring extreme temperature | Count of days at St. Paul Island with $\leq 5^{\text{th}}$ percentile mean temperatures during spring (-11.1°C) (April) | All analyses |
| Spring extreme wind | Count of days at St. Paul Island with $\geq 95^{\text{th}}$ percentile maximum wind speeds (13.6 km/hr) (April) | All analyses |
| Year | The year of nest monitoring | All analyses |
| Site | Two sites, Kigigak island and Utqiagvik | All analyses |
| Initiation date | Estimated Julian date of first egg laid | All analysis |

Table 2. Model structures of previously supported models.

| Analysis | Model | Source |
|--|---|---|
| Nest abundance | winter ice + spring wind + spring temperature | Peterson and Douglas (2004) |
| Nest abundance | winter ice + winter ice ² + spring wind + spring temperature | Peterson and Douglas (2004) |
| Apparent survival | winter ice | Flint et al. (2016) |
| Apparent survival | ice severity index | Flint et al. (2016) |
| Apparent survival and hatching success | winter ice + winter ice ² | Christie et al. (2018) and Dunham et al. (2021) |

Table 3. Number of spectacled eider nests found, nest monitoring season length, apparent nest success, number of nests used in nest survival analysis on Kigigak Island and Utqiagvik, Alaska, 1994 – 2019, and 2021.

| Year | Nests Found | Season Length | Success | Fail | Apparent Nest Success | Nest Survival Nests |
|-----------------------|-------------|---------------|---------|------|-----------------------|---------------------|
| Kigigak Island | | | | | | |
| 1994 | 84 | 143 – 189 | 58 | 20 | 0.74 | 78 |
| 1995 | 103 | 145 – 186 | 73 | 24 | 0.75 | 97 |
| 1996 | 119 | 135 – 183 | 98 | 16 | 0.86 | 114 |
| 1997 | 147 | 140 – 187 | 116 | 22 | 0.84 | 138 |
| 1998 | 111 | 149 – 189 | 95 | 12 | 0.89 | 107 |
| 1999 | 133 | 151 – 196 | 96 | 31 | 0.76 | 127 |
| 2000 | 119 | 152 – 189 | 100 | 16 | 0.86 | 116 |
| 2001 | 63 | 152 – 185 | 3 | 25 | 0.11 | 28 |
| 2002 | 146 | 145 – 209 | 114 | 24 | 0.83 | 138 |
| 2003 | 135 | 140 – 182 | 68 | 54 | 0.56 | 122 |
| 2004 | 160 | 134 – 183 | 123 | 19 | 0.87 | 142 |
| 2005 | 152 | 148 – 179 | 125 | 12 | 0.91 | 137 |
| 2006 | 179 | 151 – 189 | 139 | 29 | 0.83 | 168 |
| 2007 | 183 | 144 – 206 | 163 | 10 | 0.94 | 173 |
| 2008 | 153 | 147 – 182 | 101 | 33 | 0.75 | 134 |
| 2009 | 100 | 144 – 180 | 71 | 22 | 0.76 | 93 |
| 2010 | 115 | 147 – 180 | 83 | 19 | 0.81 | 102 |
| 2011 | 116 | 146 – 200 | 80 | 28 | 0.74 | 108 |
| 2012 | 123 | 156 – 209 | 86 | 24 | 0.78 | 110 |
| 2013 | 108 | 164 – 184 | 41 | 13 | 0.76 | 54 |
| 2014 | 100 | 153 – 201 | 70 | 14 | 0.83 | 84 |
| 2015 | 69 | 153 – 179 | 23 | 45 | 0.34 | 68 |
| 2019 | 171 | 138 – 172 | 118 | 47 | 0.72 | 165 |
| 2021 | 106 | 143 – 179 | 85 | 17 | 0.83 | 102 |
| Subtotal | 2995 | | | | | 2705 |
| Utqiagvik | | | | | | |
| 2010 | 21 | 169 – 203 | 8 | 7 | 0.53 | 15 |
| 2011 | 21 | 163 – 207 | 12 | 4 | 0.75 | 16 |
| 2012 | 26 | 166 – 205 | 9 | 6 | 0.60 | 15 |
| 2013 | 17 | 163 – 214 | 7 | 8 | 0.47 | 15 |
| 2014 | 19 | 169 – 204 | 12 | 4 | 0.75 | 16 |
| 2015 | 17 | 167 – 197 | 12 | 2 | 0.86 | 14 |
| 2016 | 25 | 162 – 204 | 8 | 10 | 0.44 | 18 |
| 2017 | 23 | 171 – 207 | 5 | 3 | 0.63 | 8 |
| 2018 | 23 | 179 – 211 | 11 | 4 | 0.73 | 15 |
| 2019 | 38 | 170 – 208 | 25 | 8 | 0.76 | 33 |
| Subtotal | 230 | | | | | 165 |
| Total | 3225 | | | | | |

Table 4. Model selection results from models examining the variation in nest initiation date of spectacled eiders at Kigigak Island (1994 – 2015, 2019, 2021) and Utqiagvik (2010 – 2019) that included winter and spring environmental variables. Every model in the set included a random effect of year on the intercept (1 | year). Models are ranked by the highest weight. K = parameter count, AIC_c = second order relative model fit value that accounts for the number of parameters in the model, ΔAIC_c = difference in AIC_c relative to samples AIC_c , and w = Akaike weight.

| Models | K | AIC_c | ΔAIC_c | w |
|---|---|-----------|----------------|------|
| WINTER ICE + site | 5 | 18,153.64 | 0.00 | 0.45 |
| SPRING EXTREME TEMPERATURE + SPRING EXTREME WIND + WINTER ICE + site | 7 | 18,154.20 | 0.53 | 0.35 |
| ICE INDEX + site | 5 | 18,155.39 | 1.73 | 0.19 |
| WINTER ICE + WINTER ICE ² + site | 6 | 18,162.89 | 9.23 | 0.00 |
| SPRING EXTREME TEMPERATURE + SPRING EXTREME WIND + WINTER ICE + WINTER ICE ² + site | 8 | 18,163.17 | 9.51 | 0.00 |
| Null | 3 | 19,226.24 | 1072.58 | 0.00 |

Table 5. Model selection results from models examining the variation in clutch size of spectacled eiders at Kigigak Island (1994 – 2015, 2019, 2021) and Utqiagvik (2010 – 2019) that included winter and spring environmental variables. Every model in the set included a random effect of year on the intercept (1 | year). Models are ranked by the highest weight. K = parameter count, AIC_c = second order relative model fit value that accounts for the number of parameters in the model, ΔAIC_c = difference in AIC_c relative to samples AIC_c , and w = Akaike weight.

| Models | K | AIC_c | ΔAIC_c | w |
|--|---|-----------|----------------|------|
| Null | 3 | 8,653.95 | 0.00 | 0.00 |
| WINTER ICE + site | 5 | 10,781.92 | 2,127.96 | 0.00 |
| ICE INDEX + site | 5 | 10,782.72 | 2,128.78 | 0.00 |
| SPRING EXTREME TEMPERATURE + SPRING EXTREME WIND + WINTER ICE + site | 7 | 10,782.81 | 2,128.86 | 0.00 |
| WINTER ICE + WINTER ICE ² + site | 6 | 10,783.12 | 2,129.16 | 0.00 |
| SPRING EXTREME TEMPERATURE + SPRING EXTREME WIND + WINTER ICE + WINTER ICE ² + site | 8 | 10,783.53 | 2,129.57 | 0.00 |

Table 6. Model selection results from daily nest survival models for spectacled eiders at Kigigak Island (1994 – 2015, 2019, 2021) and Utqiagvik (2010 – 2019) that included temporal explanatory variables. Models are sorted by highest weight. K = parameter count, AIC_c = relative model fit value that accounts for the number of parameters in the model, ΔAIC_c = difference in AIC_c between each model and the model with the lowest AIC_c , w = Aikaike weight indicating the amount of support for each model from the data, Deviance = measure of absolute model fit.

| Models | K | AIC_c | ΔAIC_c | w | Deviance |
|---|----|----------|----------------|------|----------|
| site + year + site×year + INIT + NESTAGE | 36 | 4,003.59 | 0.00 | 0.42 | 3,931.53 |
| site + year + site×year + INIT + NESTAGE + site×NESTAGE | 37 | 4,005.03 | 1.44 | 0.21 | 3,930.96 |
| site + year + site × year + INIT + NESTAGE + site×INIT | 37 | 4,005.48 | 1.89 | 0.16 | 3,931.41 |
| site + year + site×year + INIT | 35 | 4,006.68 | 3.08 | 0.09 | 3,936.61 |
| site + year + site×year + INIT + NESTAGE + site×INIT + site×NESTAGE | 38 | 4,008.80 | 3.21 | 0.08 | 3,930.72 |
| site + year + site×year + INIT + site×INIT | 36 | 4,008.58 | 4.98 | 0.03 | 3,936.51 |
| site + year + INIT + NESTAGE | 30 | 4,019.18 | 15.59 | 0.00 | 3,959.14 |
| site + year + INIT + NESTAGE + site×NESTAGE | 31 | 4,020.03 | 16.43 | 0.00 | 3,957.98 |
| site + year + INIT + NESTAGE + site×INIT | 31 | 4,020.35 | 16.75 | 0.00 | 3,958.30 |
| site + year + INIT + NESTAGE + site×INIT + site×NESTAGE | 32 | 4,021.53 | 17.94 | 0.00 | 3,957.48 |
| site + year + INIT | 29 | 4,022.31 | 18.71 | 0.00 | 3,964.26 |
| site + year + INIT + site×INIT | 30 | 4,023.52 | 19.93 | 0.00 | 3,963.48 |
| site + year + site×year | 34 | 4,032.75 | 29.15 | 0.00 | 3,964.69 |
| site + year + site×year + NESTAGE | 35 | 4,034.32 | 30.72 | 0.00 | 3,964.26 |
| site + year + site×year + site×NESTAGE | 36 | 4,036.13 | 32.53 | 0.00 | 3,964.06 |

Table 6. cont.

| Models | K | AIC _c | ΔAIC _c | w | Deviance |
|--------------------------------------|----|------------------|-------------------|------|----------|
| site + year | 28 | 4046.70 | 43.11 | 0.00 | 3,990.66 |
| site + year + NESTAGE | 29 | 4048.41 | 44.82 | 0.00 | 3,990.37 |
| site + year + NESTAGE + site×NESTAGE | 30 | 4049.84 | 46.25 | 0.00 | 3,989.80 |
| Null | 1 | 4291.89 | 291.30 | 0.00 | 4,292.89 |

Table 7. Model selection results from daily nest survival models for spectacled eiders at Kigigak Island (1994 – 2015, 2019, 2021) and Utqiagvik (2010 – 2019) that included winter and spring environmental variables. Models are ranked by the highest weight. K = parameter count, AIC_c = relative model fit value that accounts for the number of parameters in the model, ΔAIC_c = difference in AIC_c between each model and the model with the lowest AIC_c , w = Akaike weight indicating the amount of support for each model from the data, Deviance = measure of absolute fit.

| Models | K | AIC_c | ΔAIC_c | w | Deviance |
|---|---|----------|----------------|------|----------|
| SPRING EXTREME TEMPERATURE + SPRING EXTREME WIND + WINTER ICE + WINTER ICE ² + INIT + NEST AGE + site | 8 | 4,141.47 | 0.00 | 0.90 | 4,125.46 |
| SPRING EXTREME TEMPERATURE + SPRING EXTREME WIND + WINTER ICE + INIT + NESTAGE + site | 7 | 4,145.69 | 4.22 | 0.10 | 4,134.68 |
| WINTER ICE + WINTER ICE ² + INIT + NESTAGE + site | 6 | 4,157.89 | 16.42 | 0.00 | 4,145.89 |
| WINTER ICE + INIT + NESTAGE + site | 5 | 4,160.77 | 19.30 | 0.00 | 4,150.77 |
| ICE INDEX + INIT + NESTAGE + site | 5 | 4,185.93 | 44.46 | 0.00 | 4,175.93 |
| Null | 1 | 4,294.89 | 153.42 | 0.00 | 4,292.89 |