REPRODUCTIVE ECOLOGY AND ENVIRONMENTAL CHANGE: NEST SURVIVAL, NEST-SITE FIDELITY, AND NEST-SITE SELECTION OF EMPEROR GEESE ON THE YUKON-KUSKOKWIM DELTA, ALASKA

By

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CHAPTER I. INTRODUCTION

Climate change is expected to cause shifts in mean climatic conditions and increase the frequency of extreme weather events (IPCC 2014, Fischer and Knutti 2015). The effects of climate change have been observed on a global scale; however, the effects of climate change are most pronounced in the Arctic and sub-Arctic regions, as the Arctic has experienced more rapid increases in temperature and precipitation than the rest of the Northern hemisphere (Box et al. 2019), which is expected to continue under various emissions scenarios (IPCC 2014). Changes in environmental conditions due to climate change have the potential to influence demography and dynamics of species that rely on the Arctic and sub-Arctic (e.g., Dunham et al. 2021). Investigations into the effects of environmental variation on demography of species are necessary to understand the effects of climate change on Arctic biodiversity and ecology.

Geese (Tribe *Anserini*) breed primarily in the Arctic and sub-Arctic (Owen 1980), thus are likely susceptible to the effects of climate change. Due to their life history, prospective perturbation analyses (Caswell 2000) for geese often suggest that population growth rates are more sensitive to variation in survival of adults than reproductive rates (e.g., Schmutz et al. 1997, Tombre et al. 1998). However, evolution tends to favor traits that reduce variation in demographic rates to which a species is most sensitive (i.e., demographic buffering hypothesis; Hilde et al. 2020). This often causes components of recruitment to be the primary drivers of observed population growth for geese when examined using retrospective analyses (e.g., Cooch et al. 2001, Cleasby et al. 2017, Nuijten et al. 2020). The effects of climate change on reproductive success of geese may be either positive or negative depending on the reproductive rate considered and life history of the species (Nolet et al. 2020). Therefore, it is important to understand the effects of environmental variation on reproductive rates of geese when considering potential population responses to climate change.

The emperor goose (*Anser canagicus*) is a marine species endemic to coastal Alaska and Russia. Emperor geese primarily nest in western Alaska, with about 80–90% of the population nesting on the Yukon-Kuskokwim Delta (Y-K Delta; Eisenhauer and Kirkpatrick 1977). Emperor geese also nest less extensively in northeastern Russia (Kistchinski 1971, Schmutz and Kondratyev 1995) and the Seward Peninsula in western Alaska (Lewis et al. 2021). Failed breeders and nonbreeders typically undergo molt migrations to the Chukotka Peninsula in Russia or to St. Lawrence Island, Alaska (Eisenhauer and Kirkpatrick 1977, Hupp et al. 2007). Emperor geese primarily stage in lagoons on the north side of the Alaska Peninsula in autumn and spring, and winter on the Aleutian Islands, Alaska Peninsula, Kodiak Island, and in Russia (Eisenhauer and Kirkpatrick 1977, Hupp et al. 2008, Uher-Koch et al. 2021). Emperor geese are unique among North American geese in that they feed primarily on marine invertebrates in the intertidal zone during the nonbreeding season (Petersen 1983, Schmutz 1994).

Until 2016, 3-year rolling averages of annual population indices obtained from aerial surveys over spring staging areas on the Alaska Peninsula were used as the management index for emperor geese (Pacific Flyway Council 2016). These indices documented a 58% decline in the emperor goose population from 1982 to 1986 (Dau and Wilson 2015), which led to the closure of sport harvest for emperor geese in 1986 and subsistence harvest in 1987 (Pacific Flyway Council 2016). Since then, 3-year averages of the spring index documented a slow annual population growth rate, with a higher growth rate in more recent years (average 3% annually from 2005–2014; Dau and Wilson 2015, Pacific Flyway Council 2016). Supplemental indices acquired using a combination of aerial and ground-based surveys on the Y-K Delta also documented a slow population increase from 1985–2014 (average 1.8% annually; Pacific Flyway Council 2016, Fischer et al. 2018). These population indices from the Y-K Delta were adopted as the management index for emperor geese after renewal of the Pacific Flyway Council's Emperor Goose Management Plan in 2016 (Pacific Flyway Council 2016). After the spring survey population index exceeded the harvestable level of 80,000 birds in 2015, managers opened a limited fall/winter harvest (Pacific Flyway Council 2016) and spring/summer subsistence harvest (Alaska Migratory Bird Co-Management Council 2016) in 2017. Since reopening of harvest, the population index from Y-K Delta dropped below the threshold in which conservation measures needed to be considered (Pacific Flyway Council 2016, USFWS 2021). Therefore, studies examining drivers of variation in demographic rates of emperor geese are needed to understand factors limiting population growth.

Most influential studies on reproductive ecology of emperor geese in Alaska have been from before 2000. Mickelson (1975) and Eisenhauer and Kirkpatrick (1977) provided some of the first comprehensive descriptions of the reproductive ecology and life history of emperor geese on the Y-K Delta. Petersen (1990, 1992a, and 1992b) provided some of the first quantitative examinations of nest-site selection, nest survival, and survival probability of breeding female emperor geese on the Y-K Delta. Subsequent studies examined survival and ecology of broods (Laing and Raveling 1993, Schmutz 2001, Schmutz et al. 2001, Schmutz and Laing 2002), and the importance of endogenous and exogenous nutrients for breeding (Schmutz et al. 2006, Hupp et al. 2006). Long-term climate variability and habitat changes on the Y-K Delta (e.g., Terenzi et al. 2014, Jorgenson et al. 2018) have the potential to affect reproductive success of emperor geese; however, few studies have been on a large enough temporal scale to examine the influence of environmental variation on their reproductive rates. Knowledge of how emperor geese may respond to environmental variation and potential habitat changes is needed to understand how the species may respond to climate change.

Here, I used 24 years (1994–2017) of nest monitoring data from the Manokinak River, Alaska (Y-K Delta, Figure 1-1) and hierarchical models to examine the influence of environmental and individual variation on nest survival of emperor geese (Chapter II). I then used 18 years (2000–2017) of capture-mark-reencounter data from the Manokinak River to examine nest-site fidelity and how it is influenced by environmental variation and individual experience (Chapter III). Lastly, I used nest monitoring data collected in 2021 on Kigigak Island, Alaska (Y-K Delta, Figure 1-1) to examine nest-site selection and the influence nesting habitat and community characteristics on nest survival (Chapter IV). These separate but related studies will begin to fill knowledge gaps about reproductive ecology of emperor geese and help understand potential population-level responses to environmental change.

The following chapters were prepared separately for submission to peer-reviewed journals, therefore information among chapters may be redundant and formatting of each chapter may differ based on journal requirements. I was responsible for data curation, analysis, and manuscript preparation for all chapters, with valuable input and feedback from coauthors that are listed on the first page of each chapter. Due to the collaborative effort of the following works, the pronoun “we” is used throughout.

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FIGURES

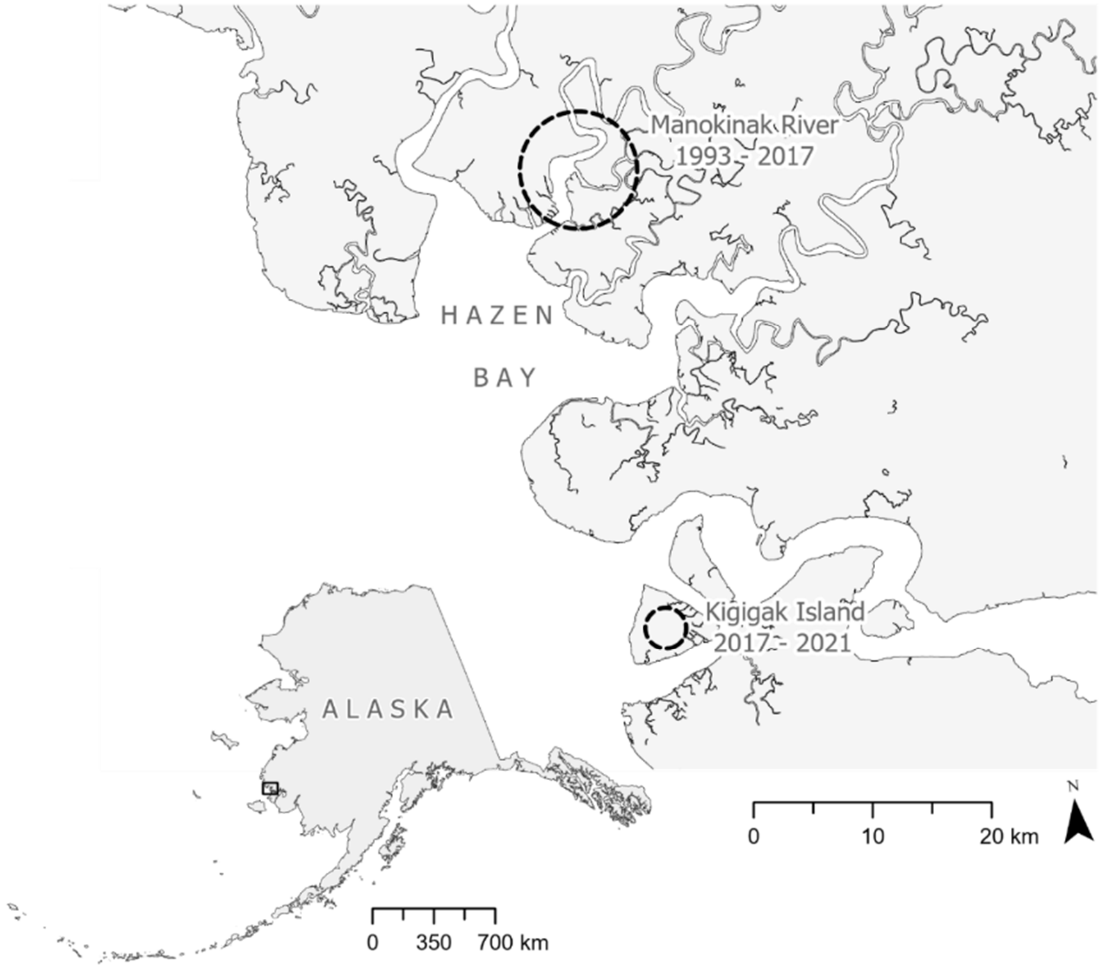

Figure 1-1. Locations of the study sites at the Manokinak River and Kigigak Island on the Yukon-Kuskokwim Delta, Alaska, USA.

CHAPTER II. FACTORS INFLUENCING NEST SURVIVAL OF EMPEROR GEESE ON THE YUKON-KUSKOKWIM DELTA, ALASKA[1]

ABSTRACT

Waterfowl productivity is often influenced by environmental conditions on the breeding grounds. For example, factors such as spring phenology, weather conditions during nesting, and local abundance of predators and alternative prey can affect productivity in Arctic-nesting goose populations. Nest survival is an important component of productivity in geese; however, the effects of breeding ground conditions on nest survival are not well understood for some species, including the emperor goose (*Anser canagicus*), a species of conservation concern that is endemic to the Bering Sea region. We estimated nest survival and examined how indices of environmental conditions, individual-level variation (e.g., nest initiation date, maximum number of eggs in the nest, nest age), and researcher disturbance influence daily survival probabilities of emperor goose nests using hierarchical models and 24 years of nest monitoring data from the Yukon-Kuskokwim Delta in western Alaska. Our results indicate that overall nest survival was generally high (μ = 0.742, 95% CRI: 0.617–0.836) and ranged from 0.283 (95% CRI: 0.137–0.443) in 2013 to 0.894 (95% CRI: 0.819–0.948) in 1995. We found that daily survival probabilities of nests were influenced by individual variation, tidal flooding events, and researcher disturbance, but were not strongly influenced by indices of spring phenology, temperature, precipitation, or fox and vole abundance on

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[1] Author list includes Thompson, J. M., B. D. Uher-Koch, B. L. Daniels, J. A. Schmutz, and B. S. Sedinger

the Yukon-Kuskokwim Delta. Furthermore, including covariates in our model reduced annual variance in daily survival probability by only ~2.1%, suggesting that important factors may not have been included. Our results suggest that environmental variation measured on large spatial or temporal scales had minimal influence on nest survival of emperor geese. We suspect that within-year variation in weather conditions and local abundance of predators and alternative prey may be important and should be considered in further analyses.

INTRODUCTION

Population growth rates of long-lived migratory bird species, such as geese (Tribe *Anserini*), are typically more sensitive to changes in adult survival rates than reproductive rates (Schmutz et al. 1997, Tombre et al. 1998, Aubry et al. 2010). However, reproductive rates are often more variable than adult survival rates for long-lived waterfowl species (Koons et al. 2014), which frequently causes recruitment to be the primary contributor to observed variation in population growth rates for geese (e.g., Cooch et al. 2001, Cleasby et al. 2017, Nuijten et al. 2020). A comprehensive understanding of the factors that influence recruitment is essential for understanding drivers of population growth for goose species and predicting population responses to global change.

The Arctic has experienced recent and rapid increases in temperature and precipitation (Box et al. 2019), which is projected to continue in climate change scenarios (IPCC 2014). Consequently, reproductive ecology of geese that breed in the

Arctic and sub-Arctic is likely susceptible to effects of climate change. For example, the onset of spring in the Arctic may become more variable with climate change, which is hypothesized to have mixed effects on reproductive rates of geese (Nolet et al. 2020). If geese are unable to adjust timing of spring migration to correspond with early spring onset, then there may be a mismatch between timing of hatch and peak forage quality for goslings (Doiron et al. 2016). This phenological mismatch can impact survival of goslings until fledging (Ross et al. 2018) and lead to reductions in gosling size (Sedinger and Flint 1991), which can have fitness consequences after fledging (Schmutz 1993, Sedinger et al. 1995). However, early spring onset also may lead to more favorable breeding conditions, with greater breeding propensity, clutch size, and nest survival (Reed et al. 2004, Dickey et al. 2008, Oudenhove et al. 2014). Years with relatively early spring onset have had higher proportions of juvenile geese after the breeding season (e.g., Alisauskas 2002, Morrissette et al. 2010), suggesting that reproductive benefits of early springs may outweigh costs, although responses are likely variable among species. Additionally, weather conditions (e.g., temperature and precipitation) during the nesting season also affect reproductive rates of geese (Dickey et al. 2008). Therefore, species-specific assessments of relationships between reproductive rates and variation in environmental conditions are needed to fully understand the potential effects of climate change on reproduction.

Nest survival, defined as the probability that a nest hatches at least one egg, is an important component of reproduction in waterfowl (e.g., Hoekman et al. 2002). Accordingly, investigating factors that influence nest survival of geese is crucial to understanding annual variation in productivity, as years of high nest failure can result in both low recruitment that year and can indirectly affect recruitment in future years (Sedinger et al. 2016). Predation is often the primary cause of nest failure in birds (Ricklefs 1969); therefore, presence and abundance of predators often directly influences nest survival of geese (Anthony et al. 1991, Reiter and Andersen 2011). Furthermore, increases in abundance of alternative prey (e.g., microtines) can lead to immediate increases in goose nest survival through functional responses in shared predators (e.g., Arctic foxes [*Alopex lagopus*] may consume proportionally more microtines in years of high abundance instead of goose eggs; Bêty et al. 2001, Bêty et al. 2002).

Some goose species defend their nest against predation by maintaining a high incubation constancy (Thompson and Raveling 1987), which they rely primarily on endogenous nutrient reserves to maintain (Ankney and MacInnes 1978, Schmutz et al. 2006). Predation of goose nests often occurs when incubating females are not present at the nest (Harvey 1971, Samelius and Alisauskas 2001). Consequently, environmental factors that affect frequency and duration of incubation breaks may influence nest survival indirectly by affecting vulnerability of nests to predation. Prolonged snow cover on the breeding grounds during late springs may limit forage availability for pre-breeding geese, forcing them to allocate more endogenous nutrients to egg formation (Hupp et al. 2018), or take longer incubation breaks in search of food (Prop and de Vries 1993), which exposes the nest to predation. This could contribute to observed higher nest survival of geese in years with early spring onset (e.g., Prop and de Vries 1993, Madsen et al. 2007, Dickey et al. 2008, Ross et al. 2017). Additionally, density of nesting geese is often higher in earlier springs (Dickey et al. 2008), which may reduce predation pressure on individual nests through predator swamping (Raveling 1989, Van Dellen and Sedinger 2020).

Weather conditions during nesting also can influence nest survival of geese, as higher temperatures and less precipitation during nesting have been associated with lower incubation constancy (Eichholz and Sedinger 1999). Furthermore, precipitation can increase availability of water on the landscape, thus reducing distances traveled to obtain water during incubation breaks (Dickey et al. 2008, Lecomte et al. 2009), potentially decreasing exposure of nests to predation. Accordingly, Dickey et al. (2008) reported a negative relationship between daily high temperature and nest survival of greater snow geese (*Chen caerulescens atlantica*), and a positive relationship between precipitation during nesting and nest survival.

The emperor goose (*Anser canagicus*) is a marine species endemic to the Bering Sea region (Schmutz et al. 2020). Aerial surveys conducted annually over spring staging areas on the Alaska Peninsula documented a population decline of over 50% in the 1980’s (Dau and Wilson 2015), prompting closure of sport and subsistence harvest starting in 1985 and 1986, respectively (Pacific Flyway Council 2016). After 3 decades, the spring survey index exceeded the threshold in which managers could consider reopening harvest in 2016, leading to the reopening of subsistence and limited sport harvest seasons in 2017 (Alaska Migratory Bird Co-Management Council 2016, Pacific Flyway Council 2016). Despite the gradual recovery, recent abundance estimates from the breeding grounds on the Yukon-Kuskokwim Delta (*hereafter,* Y-K Delta) indicated that population growth has slowed, and by 2019 the population had fallen below the threshold in which conservation measures need to be considered (23,000 birds: Pacific Flyway Council 2016, U.S. Fish and Wildlife Service 2021). Thus, detailed examinations of factors influencing vital rates are needed to understand potential drivers of population growth for this species.

No recent studies have examined factors influencing nest survival of emperor geese. Previous studies on nest survival of emperor geese on the Y-K Delta have been over small temporal scales and were not able to examine annual variation in nest survival over a broad range of environmental conditions (Eisenhauer and Kirkpatrick 1977, Petersen 1992). We used 24 years of nest monitoring data from a breeding site on the Y-K Delta to provide contemporary estimates of nest survival for emperor geese and determine the influence of environmental and individual variation on daily survival probabilities (DSP) of nests. We predicted that DSP of emperor goose nests would be higher in years with early spring onset due to better body condition of individuals and higher abundance of conspecific and heterospecific geese to buffer predation pressure. Additionally, we predicted that DSP would be higher in cooler and wetter years due to higher incubation constancy. Lastly, we predicted that DSP of nests would be higher when abundance of Arctic foxes was low and/or abundance of microtines (i.e., voles) was high due to decreased predation pressure on emperor goose nests.

MATERIALS AND METHODS

We monitored nests of emperor geese at the Manokinak River (165.10°W, 61.21°N; Figure 2-1) on the Y-K Delta in western Alaska from 1994–2017. The study area is located approximately 9 km from the mouth of the river and 190 km northwest of Bethel, Alaska. The study area is at low elevation (<5m above sea level), and is interspersed with many small, shallow freshwater ponds and tidal sloughs. Vegetation communities in the study area consisted primarily of meadows dominated by salt tolerant graminoids (e.g., *Carex ramenskii*) and dwarf-scrub plants (Kincheloe and Stehn 1991, Jorgenson 2000). The primary nest predators in the study area are Arctic foxes, parasitic jaegers (*Stercorarius parasiticus*), and glaucous gulls (*Larus hyperboreus*).

We searched 14 contiguous plots (~23 km^2) annually for all emperor goose nests on foot by systematically searching all areas within a plot that were able to hold a nest (i.e., not over water or mud). We searched additional areas outside of the 14 plots in some years, however we restricted our analyses to nests with known locations found within the 14 plots to eliminate confounding between study area extent and year in our analyses. Additionally, we did not search plots in 1999, and nests were not monitored until hatch in 1998 and 2005, so we did not consider these years in our analyses.

Once we located a nest, we aged eggs using floating (Westerkov 1950) or candling (Weller 1956) and recorded coordinates of nests using handheld GPS receivers. After initial nest checks, we revisited nests at irregular intervals until a fate could be determined (hatched, preyed upon, abandoned, etc.). We considered a nest successful if pipped eggs, goslings, or eggshell fragments with intact detached membranes were found in the nest. We considered a nest to be preyed upon if eggs in the nest were broken without sign of detached membranes or if all eggs were missing, and we considered a nest abandoned if all eggs in the nest were cold and a female was not present. For part of a concurrent mark-resight study to estimate adult female survival probabilities, we trapped incubating females on the nest using bow-net traps (Salyer 1962) or mist-net traps (Bacon and Ervard 1990) and marked them with a U.S. Geological Survey metal leg band and a plastic tarsal band with a 3-character alphanumeric code.

We considered a nest to be successful on the day that the first egg in the nest was pipped. We predicted hatch dates for each visit using nest ages and assuming a 24-day incubation period (Eisenhauer and Kirkpatrick 1977, Petersen 1992), and attempted to revisit nests on or near their predicted hatch date. In instances when hatch was not directly observed, we estimated hatch dates by averaging the predicted hatch dates from all visits to a nest in which nest ages were obtained. If egg ages were never obtained for a nest (n = 31), we assigned them the average hatch date for the year the nest was found. If a nest was still active past its average estimated hatch date, then we used the predicted hatch date from the last nest check. We considered a nest initiated on the day the first egg was laid, and estimated nest initiation dates by back-calculating from the estimated hatch date for each nest, assuming an egg-laying rate of 1.2 days/egg and that geese began incubating as soon as the last egg was laid (Eisenhauer and Kirkpatrick 1977, Petersen 1992). Using the back-calculated initiation dates, we estimated nest age at the time a nest was found (i.e., days since initiation) by subtracting the date the nest was found from its estimated initiation date. If the estimated age when the nest was first found was less than the length of the laying period for that nest, then we considered the female to be laying upon nest discovery and recalculated the nest initiation date using the number of eggs on the first visit. This approach allowed for more accurate representation of nest ages for nests found during laying. When calculating initiation dates, we considered clutch size to be the maximum number of eggs found in a nest. Several nests had unrealistic clutch sizes (>10; *n* = 12), suggesting potential intraspecific nest parasitism which is common in breeding emperor geese (Petersen 1992, McCloskey 2013). Therefore, we assigned those nests the median clutch size for the year in which the nest was located to avoid extreme bias when estimating nest initiation date.

We generated encounter histories for each nest using the first day the nest was found (I), the last day the nest was seen alive (J), the last day the nest was checked (K), and the nest fate (hatched or failed). For successful nests, $J = K$ and is the estimated or observed hatch date, and for failed nests K is the predicted hatch date if the nest was found failed after its predicted hatch date (Dinsmore et al. 2002). We standardized dates in encounter histories by subtracting the ordinal date of the first nest found among all years (20 May for regular years, 19 May for leap years). We right censored nests that were visited more than once but were not monitored until hatch; therefore, J and K are the date of the last nest check for those nests. We censored nests that were only checked once and nests that were destroyed by observers. Additionally, we censored nests that failed due to an inviable or addled clutch because we could not be certain when the eggs became inviable.

To estimate DSP of emperor goose nests and examine factors influencing DSP, we constructed nest survival models and analyzed them in a hierarchical Bayesian framework. Descriptions and data sources for covariates we included to determine potential influences on nest survival of emperor geese are summarized in Table 1. We modeled period survival (S; S = 1 for nests that survived the period, S = 0 for nests that failed during the period) for the interval from I to $J-1$ and from J to $K-1$ for each individual nest (i) as Bernoulli processes with the success probabilities equal to the product of a vector of DSPs for each day (j) and nest combination as follows:

$$S_i^{I:J-1} \sim Bernoulli(\prod_I^{J-1} DSP_{i,j}), \tag{1}$$

$$S_i^{J:K-1} \sim Bernoulli(\prod_J^{K-1} DSP_{i,j}). \tag{2}$$

We modeled variation in DSP for each combination of nest, day, and year (t) as a linear function of covariates using a generalized linear mixed model as follows:

$$logit\left(DSP_{i,j,t}\right) = \alpha + \sum \beta_x \boldsymbol{X}_{i,j,t,x} + \varepsilon_t, \tag{3}$$

$$\varepsilon_t \sim Normal(0, \sigma_t^2), \tag{4}$$

where α is mean DSP on the logit scale, β_x is a vector of regression coefficients, $\boldsymbol{X}_{i,j,t,x}$ is a matrix of covariates corresponding to each regression coefficient for each nest, day, and year combination, ε_t is random annual variation on the logit scale which we assumed was normally distributed, and σ_t^2 is an annual variance term.

To obtain unbiased estimates of nest survival and a baseline temporal variance estimate to compare with our covariate model (Kéry and Schaub 2012), we fit a model with linear and quadratic effects of nest age, trapping occasions, and random annual variation following equations (3) and (4), where β_x was a vector of 3 regression coefficients and $\boldsymbol{X}_{i,j,t,x}$ was a matrix of x = 3 covariates. We z-standardized nest age using the population mean and standard deviation. Due to limited nest monitoring data during egg laying in some years, we assumed the relationship between DSP and nest age was the same among years. To avoid biases associated with estimating nest survival with a constant DSP (Weiser 2021), we derived estimates of nest survival and associated uncertainty for each year as the product of age-and-year-specific DSP for ages 1–28 (i.e., the exposure period for an emperor goose nest with a five-egg clutch).

To examine the influence of environmental and individual variation on DSP, we fit a global a priori model with covariates from Table 1 and random annual variation following equations (3) and (4), where β_x was a vector of 14 regression coefficients and $\boldsymbol{X}_{i,j,t,x}$ was a matrix of x = 14 covariates. We tested for collinearity of covariates by calculating Pearson correlation coefficients (r) for all pairs of continuous variables. We included quadratic terms for nest age, initiation date, and maximum number of eggs incubated. We z-standardized all annual covariates (thaw degree days, temperature, precipitation, fox , vole; Table 1) using the mean and standard deviation among years. We z-standardized individual nest initiation date and maximum number of eggs incubated using the annual mean and standard deviation; therefore, regression coefficients for these covariates represent effects of deviation from the annual mean for each individual covariate rather than the population mean. We z-standardized nest age using the population mean and standard deviation, as nest age is deterministic and does not vary by year. We report the proportion of posterior samples on the same side of 0 as the mean (f) for each coefficient, and interpret f as the probability of a positive or negative relationship existing. We interpreted $f \geq 0.90$ as strong evidence for a relationship, and $0.90 > f \geq 0.85$ as moderate evidence for a relationship. To determine how much annual variation in DSP was explained by our covariates, we used the annual variance from the random year term in our model without covariates to calculate the percent reduction in annual variance when covariates were included in the model (Kéry and Schaub 2012, Dunham et al. 2021). To visualize the effects of influential covariates, we derived model-based predictions for each influential covariate with all other covariates held constant at their mean for continuous covariates, and in the absence of an effect for daily indicator variables (coded as 1 or 0 on days of occurrence; flood, visit, trap; Table 1). Predictions for maximum number of eggs incubated were based on 2–14 eggs and were z-standardized using the mean and standard deviation from 1997, which was closest to the mean DSP among years.

We fit models using JAGS (Plummer 2003) through the “jagsUI” package (Kellner 2021) in R version 4.0.3 (R Core Team 2021). We modeled intercepts on the probability scale using $Uniform(0,1)$ priors, regression coefficients using $Normal(0,100)$ priors, and standard deviations of random effects using $Uniform(0,5)$ priors. We sampled three Markov Chain Monte Carlo (MCMC) chains of 75,000 iterations, discarded 2,000 iterations as burn-in, and retained every fifth iteration. We assessed convergence of

MCMC chains by inspecting trace plots for proper mixing and evaluating Gelman-Rubin test statistics ($\hat{R}$; Brooks and Gelman 1998). We summarized posterior distributions using means and 95% credible intervals (95% CRI) and report those in the results.

RESULTS

A total of 3,215 emperor goose nests were monitored in the 14 core plots and included in analyses. Of those nests, a total of 2,427 hatched at least one egg, 378 failed, and 410 were right censored at the last check date. An average of 152 nests were found in core plots each year, ranging from 69 in 2001 to 227 in 1995 (Figure 2-2). Mean nest initiation date was earliest in 2016 (10 May) and latest in 2012 (3 June). Median number of eggs in the nest varied between 4 and 5 eggs. Average age at initial nest discovery for the entire study period was 14 days, which was about halfway through the exposure period for a 4 or 5 egg clutch. Nests were visited an average of 2.54 times, and a total of 536 of the nesting females in our sample were trapped on the nest before hatch.

Proportion of thaw degree days in April and May varied from 0.86 in 2004 to 0.16 in 2001 and was highly correlated with mean nest initiation dates (r = -0.898). Average temperatures for the mean exposure period in Hooper Bay varied from 3.85°C in 2014 to 9.79°C in 2002, and total precipitation in Bethel for the mean exposure period varied from 9.7mm in 2001 to 69mm in 2012. Proportion of random nest plots with sign of fox and vole ranged from 0.89 in 2001 to 0.16 in 1994 and 0.78 in 2000 to 0.11 in 1994, respectively (Fischer et al. 2017).

Trace plots and $\hat{R}$ values indicated that chains adequately converged for both models. Mean DSP (α) of nests from our model with only age, trapping, and random year effects was 0.996 (95% CRI: 0.994–0.997), with an annual variance of 0.524 (95% CRI: 0.245–1.049) on the logit scale. Mean overall nest survival across the 21-year study period was 0.742 (95% CRI: 0.617–0.836; Figure 2-3) and ranged from 0.283 (95% CRI: 0.137–0.443) in 2013 to 0.894 (95% CRI: 0.819–0.948) in 1995 (Figure 2-3).

Mean DSP from our covariate model was 0.998 (95% CRI: 0.997–0.999), with an annual variance of 0.513 (95% CRI: 0.198–1.171), indicating inclusion of covariates only explained 2.1% of the annual variance in DSP from our previous model without environmental covariates. We did not find strong support for an effect of proportion of thaw degree days in April and May (f = 0.742), average daily temperature during the mean exposure period (f = 0.578), total precipitation during the mean exposure period (f = 0.781), or our indices of fox occurrence (f = 0.660) and vole occurrence (f = 0.536) on DSP of nests in our study (Figure 2-4A). We found strong support for an effect of major summer floods on DSP of nests (f = 1.000; Figure 2-4B), with the lowest overall nest survival estimates corresponding to the years of major flood events (2010 and 2013; Figure 2-3). We found strong support for a quadratic effect of nest age (f = 1.000 for linear and quadratic terms), total number of eggs incubated (f = 1.000 for linear and quadratic terms), and nest initiation date (f = 1.00 for linear term, f = 0.958 for quadratic term) on DSP (Figure 2-4A). Lastly, we found support for declines in DSP on days with observer visits (f = 1.000) and trapping occasions (f = 1.000; Figure 2-4B).

Our model-based predictions suggest that DSP increased with the number of eggs in the nest but began to decline as the number of eggs exceeded 10 (Figure 2-5A), and DSP was lowest for birds that initiated their nest before the mean nest initiation date (Figure 2-5B). Additionally, DSP was lowest during the laying period (days 1–5), increased until mid-incubation, and began to decline again toward late incubation (~day 20; Figure 2-5C). With all other covariates held constant at their mean, visiting a nest decreased DSP for that day by 0.007, flooding events decreased DSP by 0.028, and trapping a female on the nest decreased DSP by 0.056 (Figure 2-5D). When scaled to nest survival, the predicted probability of a nest hatching at least one egg was 0.958 (95% CRI: 0.937–0.975) in the absence of visits, trapping, or flooding and with all other covariates held constant at their mean. Nest survival declined to 0.945 (95% CRI: 0.921–0.963) when a nest was visited twice, 0.918 (95% CRI: 0.881–0.946) when a nest was visited twice and flooded, and 0.891 (95% CRI: 0.847–0.926) when a nest was visited twice, and the female was trapped.

DISCUSSION

Understanding variation in population growth rates of a species requires both estimates of vital rates and knowledge of factors influencing variation in vital rates. In general, we found that nest survival of emperor geese was high throughout our study period (Figure 2-3). Surprisingly, our results indicate that indices related to regional climate and abundance of predators and alternative prey included in our model did not influence daily nest survival of emperor geese at the Manokinak River, although individual variation and flooding events appeared to be important.

Advancing spring phenology due to climate change has been observed in the Arctic and is predicted to continue as the Arctic warms (Box et al. 2019, IPCC 2014), which will likely affect reproductive ecology of geese that are adapted to the short growing seasons associated with Arctic ecosystems (Owen 1980, Nolet et al. 2020). Emperor geese undergo comparatively short migrations from their spring staging grounds on the Alaska Peninsula to their breeding grounds on the Y-K Delta, thus may use weather conditions on the staging grounds to cue migration (Petersen 1992, Hupp et al. 2006). Accordingly, later initiation dates in years with later spring onset have been reported in previous studies of emperor geese (Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Petersen 1990). Similarly, we observed that mean nest initiation dates of emperor geese at the Manokinak River are negatively correlated with the proportion of thaw degree days in April and May; however, we did not find strong evidence that spring phenology directly affected nest survival. Emperor geese maintain a high incubation constancy (~99.5%; Thompson and Raveling 1987) that is influenced by female body condition, with females in worse body condition taking more incubation breaks to feed (Schmutz et al. 2006). Because emperor geese can delay migration from spring staging grounds to breeding grounds in years of late spring onset (Petersen 1992, Hupp et al. 2006), they can acquire additional endogenous nutrient reserves needed for incubation rather than arriving on the breeding grounds before forage is available. Furthermore, individuals may delay migration or nest initiation until they have attained sufficient nutrient reserves (Hupp et al. 2006). Thus, at the population level, body condition at the onset of incubation may not differ significantly between early and late springs, or annual variation in body condition at the population level may have negligible effects on incubation constancy and subsequently nest survival. In addition to affecting body condition, earlier onset of spring may lead to greater breeding propensity and subsequent density of nesting geese on the landscape, which could buffer predation pressure on individual nests (Dickey et al. 2008). It is unclear if breeding propensity of geese on the Y-K Delta is affected by variation in spring phenology; however, given long-term changes in goose abundance on the Y-K Delta (Fischer et al. 2017, 2018, Sedinger et al. 2019), it is unlikely that spring phenology has been a significant driver of annual variation in nest density during our study period. Thus, although variation in spring phenology may not influence on nest survival of emperor geese under the range of conditions we observed, it may influence other reproductive parameters (e.g., breeding propensity, clutch size, gosling survival) that we did not evaluate in our study (Nolet et al. 2020), warranting further examinations.

Weather conditions during nesting have the potential to influence nest survival of geese, although the directions of effects are inconsistent among species and populations (e.g., Dickey et al. 2008, Lecomte et al. 2009, Ross et al. 2017, Layton-Matthews et al. 2020). Because we did not directly measure temperature and precipitation at our study site, we summarized temperature and precipitation at Hooper Bay and Bethel over the mean exposure period to represent annual variation in weather during nesting, which we expected would be similar across the Y-K Delta. Accordingly, our results suggest that DSP of emperor goose nests was not influenced by annual variation in temperature or precipitation on the nesting grounds. Hooper Bay is ~65 km north of our study site on the Bering Sea coast; therefore, we believed that annual variation in mean temperature during the exposure period was representative of conditions at our study site (Figure 2-1). However, total precipitation in Bethel may not have been fully representative of conditions at our study site, as Bethel is ~190 km southeast of our study site (Figure 2-1). Therefore, we caution that our lack of support for this variable may be due to inadequate representation of study area conditions rather than lack of biological effect. Additionally, daily variation in temperature and precipitation may influence DSP (e.g., Kellett and Alisauskas 2019) as frequency and duration of incubation breaks are often influenced by daily patterns in ambient temperature or precipitation (Eichholz and Sedinger 1999, Meixell and Flint 2017), although this has not been observed for emperor geese (Thompson and Raveling 1987). Summarizing temperature and precipitation across the mean exposure period also precluded us from evaluating the potential impact of extreme weather events on nest survival (besides the two years with observed major flooding). We recommend further studies of the effects of weather during the nesting season on nest survival of emperor geese measure daily temperature, precipitation, and extreme weather events at the study site for inclusion as daily covariates.

Summer flooding events resulting from storm surges during the nesting season on the Y-K Delta often occur on small scales but can greatly affect waterfowl productivity (Hansen 1961, Flint and Grand 1996). Our results indicate that the observed major flooding events on the study area directly affected DSP of emperor goose nests as the two years with the lowest nest survival had major flooding events; however, we emphasize that our flooding covariate was based only on observations from the study area and not quantitative data. Additionally, 15 nests that failed in 2013 were expected to hatch on the day of the flood. Therefore, we suspect that the effect of flooding may have been underestimated in our study because we were not able to account for smaller floods that affected nests at lower elevations, and our flooding covariate may not have accounted for some nests that could have failed immediately before hatch. It is unclear whether storm surges while birds are nesting during spring and early summer will become more frequent in climate change scenarios; however, larger flooding events resulting from storm surges in autumn are common on the Y-K Delta and are expected to occur more frequently as sea levels rise and storms become more common (Jorgenson and Ely 2001, Terenzi et al. 2014). These floods have the potential to alter nesting and brood rearing habitat on the Y-K Delta (Jorgenson et al. 2018), which may also indirectly affect productivity of emperor geese.

We were surprised that our index of fox abundance on the Y-K Delta did not influence nest survival of emperor geese in our study, as Petersen (1992) reported extreme localized nest failure for emperor geese at a different site on the Y-K Delta in years with high fox abundance. Similarly, Dunham et al. (2021) did not find evidence for a relationship between the fox index we used and nest survival of spectacled eiders (*Somateria fischeri*) on the Y-K Delta; however, Rizzolo et al. (2014) found evidence for a negative relationship between the fox index we used and nest survival of red-throated loons (*Gavia stellata*) on the Y-K Delta. Emperor geese are more capable of defending their nests against foxes than smaller geese like cackling geese (*Branta hutchinsii* *minima*) and black brant (*Branta bernicla nigricans*; Mickelson 1975, Eisenhauer and Kirkpatrick 1977). Further, foxes may concentrate search efforts in areas with greater densities of nests, such as black brant colonies (Stickney 1991). Therefore, we speculate that fox abundance may not be a significant driver of annual variation in nest survival for emperor geese, although years of extremely high fox abundance may lead to more nest failure. Additionally, eggs may be the primary source of food for Arctic foxes on the Y-K Delta regardless of vole abundance (Stickney 1991), which could explain our lack of support for an effect of the index of vole abundance on DSP of nests. We emphasize that the indices of fox and vole abundance included in our model were for the entire coastal zone of the Y-K Delta (Fischer et al. 2017) and may not reflect local abundance of foxes and voles at our study area; therefore, additional small-scale studies are needed to fully understand the interaction between vole abundance, fox abundance, and reproductive success of geese on the Y-K Delta. We also were unable to account for differences in abundance of avian predators like glaucous gulls or parasitic jaegers, which also prey upon emperor goose nests (Eisenhauer and Kirkpatrick 1977), although we suspect that predation of emperor goose nests by avian predators was likely consistent among years and most predation from avian predators was partial predation rather than total clutch loss (Mickelson 1975, Flint and Grand 1996).

Previously reported relationships between nest initiation date and nest survival of geese have been mixed, with support for both curvilinear relationships (e.g., Findlay and Cooke 1982, Lepage et al. 2000, Grand et al. 2006) and linear declines in nest survival with nest initiation date (Baldwin et al. 2011). We found evidence that DSP was lower for birds that initiated their nest before the annual mean. We hypothesize that, although emperor geese do not nest colonially, they may benefit from synchronous nesting with heterospecific geese, in which peak initiation among species on the Y-K Delta differ by an average of ~2 days (Fischer et al. 2017). Therefore, geese that initiate nests earlier in the season may be more susceptible to predation due to lower densities of conspecific and heterospecific geese to buffer predation pressure. We were surprised to find that DSP of emperor goose nests remained high for birds that initiated their nest after the annual mean, as previous studies report declines in nest survival with later nest initiation dates (Baldwin et al. 2011). Consistent with Petersen (1992), we found that emperor goose nests with fewer eggs had lower DSP (Figure 2-5A), and the maximum number of eggs and standardized initiation date for emperor goose nests were moderately correlated (r = -0.654). We suspect that variation in DSP for birds that initiate their nest later may be accounted for by our maximum number of eggs in the nest variable, making the relative importance of these variables difficult to interpret. Furthermore, intraspecific nest parasitism is common in emperor geese (McCloskey 2013, Schmutz et al. 2020) and often goes undetected, meaning estimates of initiation dates for parasitized nests may be biased. While we attempted to account for extreme cases of nest parasitism (>10 eggs in the nest) when estimating nest initiation dates, we were unable to account for less extreme cases that are likely more common, although intraspecific nest parasitism has not been shown to influence nest survival for emperor geese (McCloskey 2013, Schmutz et al. 2020). Additionally, we were unable to account for partial predation of nests before nests were located, which could also lead to bias in estimates of nest initiation dates and maximum number of eggs in the nest.

While we attempted to provide unbiased estimates of nest survival by accounting for variation in DSP with nest age (Weiser 2021), we emphasize that relatively few nests were monitored at early ages (e.g., during egg laying), and nests were not monitored at early ages every year. Therefore, we assumed the relationship between DSP and nest age was consistent among years, which may not be the case, and if so, we suspect that annual differences in nest survival could be underestimated, particularly if the effects of environmental variation on DSP are more apparent during laying. Additionally, we were surprised that DSP decreased later in incubation, as Thompson and Raveling (1987) report higher incubation constancy for emperor geese towards the end of incubation. A decline in DSP late in incubation also was observed in dusky Canada geese (*Branta canadensis occidentalis*; Grand et al. 2006), which the authors attributed to a potential decline in nest attentiveness as incubation progressed. Eichholz and Sedinger (1999) also report a decline in incubation constancy throughout the incubation period of black brant. We speculate that potential changes in incubation or predator behavior late in incubation could explain this result; however, unmodeled observer effects due to increased activity in plots during late incubation or smaller-scale late season flooding events could contribute as well.

Researchers displacing females from nests can expose the nest to predation, which may bias estimates of DSP and nest survival if not mitigated or addressed in analyses (Rotella et al. 2000). Declines in DSP following observer visits (Rizzolo et al.

2014, Meixell and Flint 2017) and trapping events (Uher-Koch et al. 2015) have been documented in water birds, although other studies report no effects (e.g., Sedinger 1990, Kellett and Alisauskas 2019). We found evidence that visiting nests marginally decreased DSP (Figure 2-5D) and subsequently nest survival. Trapping females on the nest had a stronger effect on DSP, likely due to increases in displacement time or higher probability of nest abandonment following trapping events; however, only a sample of females were trapped during incubation each year. Additionally, given that declines in DSP with nest age were supported in our model despite accounting for trapping effects, some nesting females that were trapped may have failed their nesting attempt later in incubation regardless of whether they were trapped. Thus, the effects of trapping on nest fate of individuals within a year were likely minimal, although DSP was biased low (Gibson et al. 2015). We suggest that study designs involving nest monitoring consider alternatives to nest visits, such as cameras and temperature loggers (e.g., Thermochron iButtons; Maxim, Sunnydale, CA), which can reduce disturbance on nests while simultaneously increasing temporal resolution of data and decreasing costs of collection (Hartman and Oring 2006, Sutti et al. 2014). Additionally, we suggest studies that include trapping of females on nests consider minimizing nest trapping to reduce disturbance while still acquiring sufficient sample size to answer research questions.

Since closures of harvest in the mid 1980’s, the emperor goose population in Alaska exhibited a slow, albeit positive, population growth rate (Pacific Flyway Council 2016). Reasons for the slow population growth rate are not well understood but may be attributed to life history characteristics including low juvenile survival (Schmutz et al.

1994), delayed breeding until at least 3 years of age (Schmutz 2000), and infrequent breeding thereafter (Schmutz and Morse 2000, Hupp et al. 2006). Our results indicate that survival of emperor goose nests is high, consistent with previous reports from other study areas on the Y-K Delta (Petersen 1992), suggesting nest survival may not limit population growth, although years of low nest survival may contribute to variation in recruitment. Additionally, our results suggest that annual variation in environmental conditions measured in our study did not influence nest survival, although flooding from storm surges may cause localized nest failure if they become more frequent. Similar long-term investigations are needed to monitor changes in vital rates with climate change, as more variable and extreme weather conditions may have a stronger impact on vital rates and population growth in the future. Furthermore, to fully understand the complex effects of environmental variation on productivity and population growth of emperor geese, further studies should consider other components of reproduction.

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FIGURES

Figure 2-1. Location of the Manokinak River study site (black dashed circle) on the Yukon-Kuskokwim Delta, Alaska, USA. Locations of Hooper Bay and Bethel, Alaska, where temperature and precipitation data were recorded, are marked with black points.

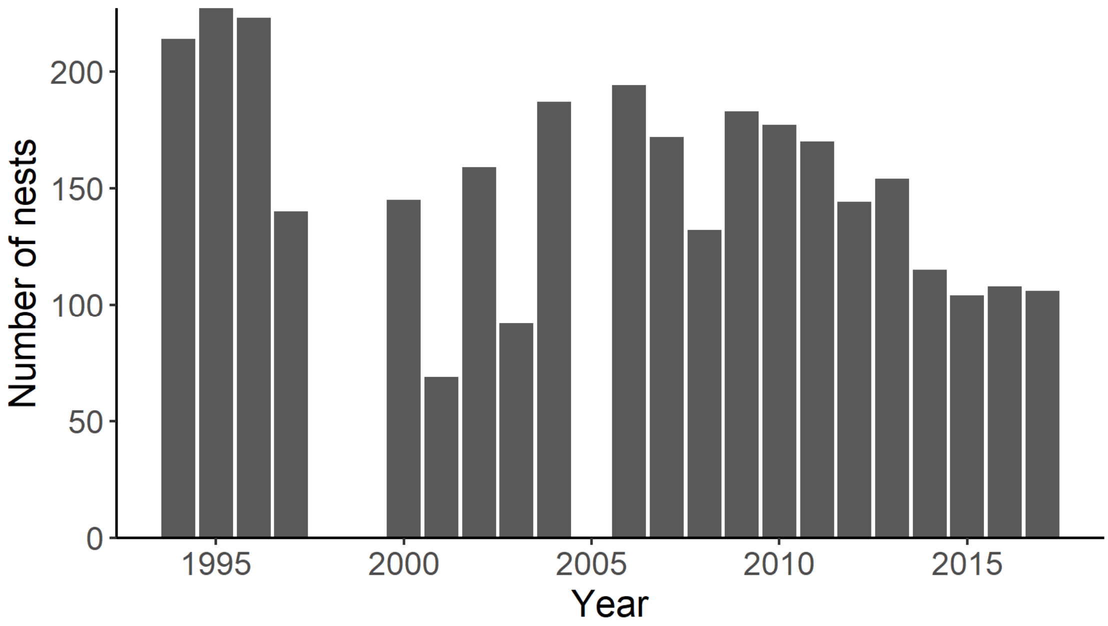

Figure 2-2. Number of emperor goose nests monitored at the Manokinak River, Alaska, USA from 1994–2017 and included in nest survival analyses. Plots were not searched in 1999 and nests were not monitored until hatch in 1998 and 2005.

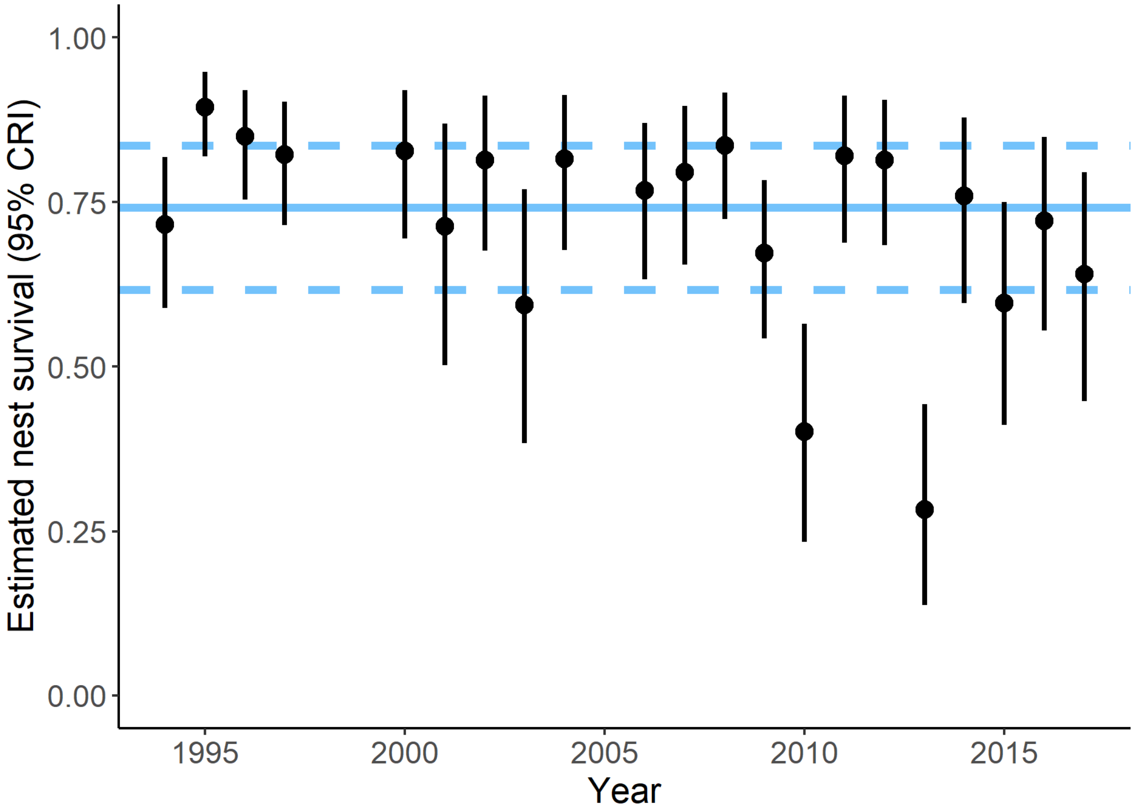

Figure 2-3. Estimates of overall nest survival and 95% credible intervals (CRI) for emperor geese at the Manokinak River, Alaska, USA from 1994–2017. Blue solid line is mean nest survival for the study period, and blue dashed lines are 95% credible intervals of the mean. Nest survival was not estimated for 1998, 1999, or 2005.

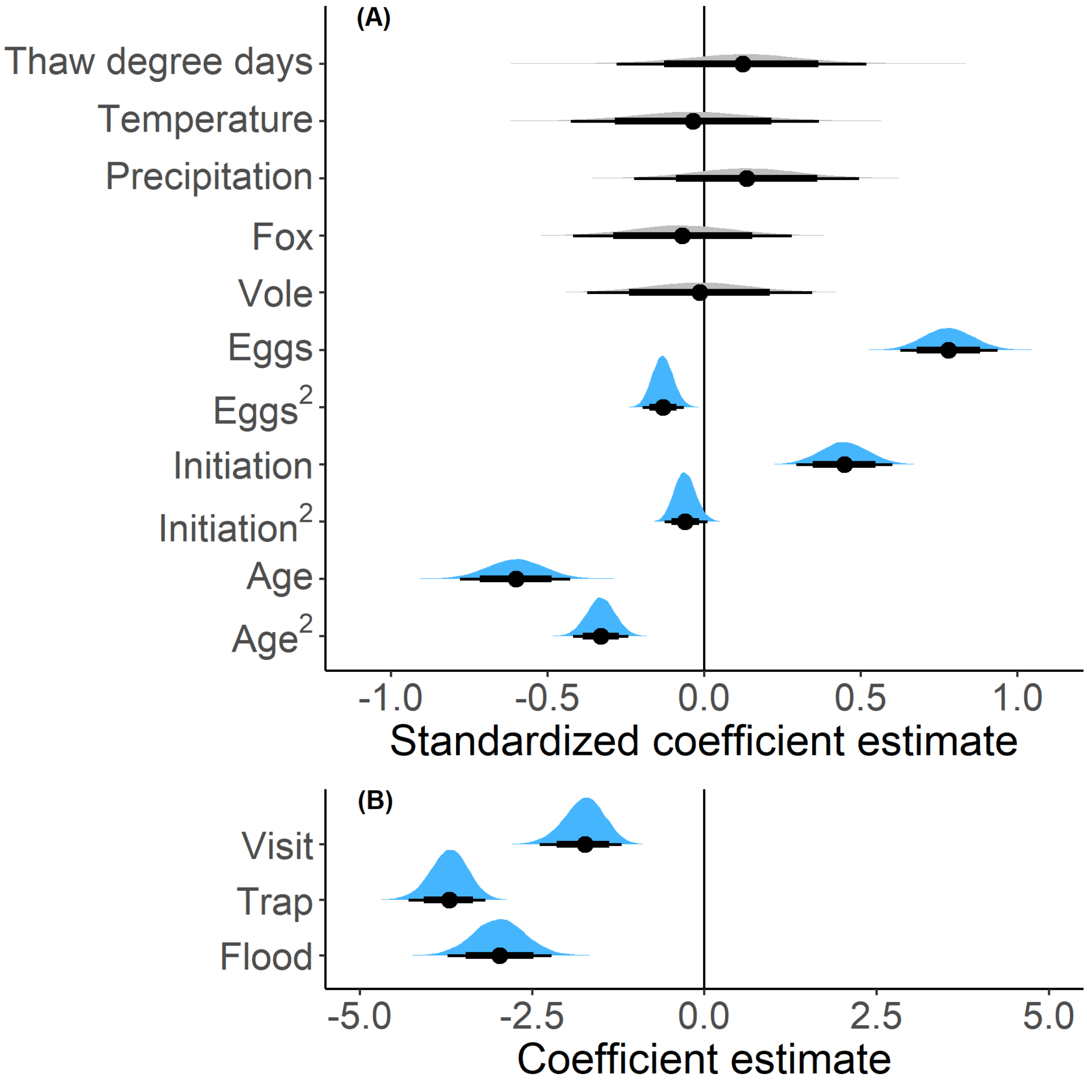

Figure 2-4. Posterior distributions of regression coefficients from our hierarchical nest survival model for (A) standardized and (B) non-standardized covariates used to model variation in daily survival probability of emperor goose nests monitored at the Manokinak River, Alaska, USA from 1994–2017. Points are means of posterior distributions, thick lines are 80% credible limits, and thin lines are 95% credible limits. Distributions shaded in blue had strong support for an effect ($f \geq 0.90$), while distributions shaded in grey had weak or no support for an effect ($f < 0.85$).

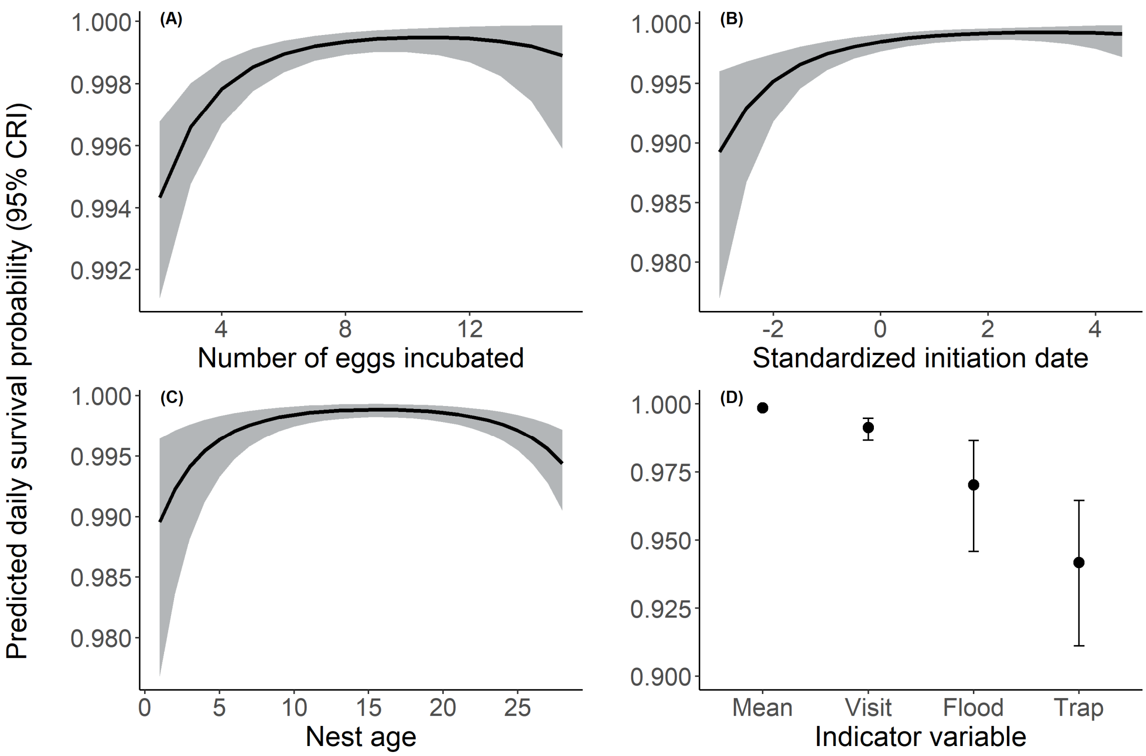

Figure 2-5. Predicted daily survival probability and 95% credible intervals (95% CRI) of emperor goose nests monitored at the Manokinak River, Alaska, USA from 1994–2017 in relation to (A) the maximum number of eggs incubated, (B) standardized nest initiation date, (C) nest age, and (D) indicator variables (nest visits, flooding, and trapping). Predictions were derived from a hierarchical nest survival model with all other variables held constant at their means. Predictions for maximum number of eggs incubated were based on 2–14 eggs and standardized using the mean and standard deviation from 1997, which was closest to the mean DSP among years.

TABLES

Table 2-1. Descriptions and data sources of covariates used in nest survival model for emperor goose nests monitored at the Manokinak River, Alaska, USA from 1994–2017. Only linear effects of covariates were tested for each variable unless otherwise specified.

Type	Variable abbreviation	Description	Source
Annual	Thaw degree days	Proportion of thaw degree days (average temperature >0°C)[c] in April and May in Hooper Bay, Alaska	National Oceanic and Atmospheric Administration (2021a)
	Temperature	Average daily temperature during the mean exposure period[d] in Hooper Bay, Alaska	National Oceanic and Atmospheric Administration (2021a)
	Precipitation	Total precipitation (mm) during the mean exposure period[d] in Bethel, Alaska	National Oceanic and Atmospheric Administration (2021b)
	Fox	Proportion of random nest plots on coastal zone of the Y-K Delta that have active sign of fox[e]	Fischer et al. (2017)
	Vole	Proportion of random nest plots on coastal zone of the Y-K Delta that have active sign of vole[f]	Fischer et al. (2017)
Individual	Eggs[a,b]	Maximum number of eggs incubated for each nest monitored	This study
	Initiation[a]	Initiation date for each nest monitored	This study
Daily	Age[a]	Age of a nest on each day a nest was monitored	This study
	Flood	Major flooding events on 18 June 2010[g] and 29 June 2013	Fischer et al. (2010, 2014)
	Visit	Day of visits to a nest before hatch	This study
	Trap	Day of trapping events before hatch	This study

[a] Both linear and quadratic terms were tested

[b] Number of eggs is not analogous to clutch size due to high degree of intraspecific nest parasitism in emperor geese (Schmutz et al. 2020)

[c] Proportion was used due to missing data for some days

[d] Mean exposure period was defined as the mean initiation date through the mean hatch date for each year

[e] Active fox sign included direct sightings, tracks, trails, fur, and active dens; includes arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*)

[f] Active vole sign included direct sightings, scat, tunnels, and runs

[g] Date of flood was approximated using tide gauge data from Hooper Bay, Alaska

CHAPTER III. EFFECTS OF PREVIOUS REPRODUCTIVE SUCCESS AND ENVIRONMENTAL VARIATION ON NEST-SITE FIDELITY OF EMPEROR GEESE[2]

ABSTRACT

Nest-site fidelity is a common strategy in birds and is believed to be adaptive due to familiarity with local resources. Returning to previously successful nest sites (i.e., win-stay/lose-shift strategy; WS-LS) may be beneficial when habitat quality is spatially variable and predictable; however, variation in environmental conditions, such as spring phenology, may constrain dispersal decisions in Arctic-nesting species despite previous reproductive success. We used 18 years (2000–2017) of capture-mark-reencounter data and multistate models to examine fine-scale nest-site fidelity in emperor geese (*Anser canagicus*) on the Yukon-Kuskokwim Delta, Alaska. Our objectives were to estimate nest-site dispersal probabilities for emperor geese, determine whether dispersal is affected by previous nest fate, spring phenology, and major flooding events on the study area, and determine if nest-site fidelity is adaptive in that it leads to higher nest survival. Our sample consisted of 1,256 encounters of 536 marked emperor geese from 2000–2017, and we defined dispersal as moving ≥200m from an individual's nest site in the previous year. Dispersal probability was 0.337 (95% CRI: 0.283–0.393) for individuals with successful nests and 0.477 (95% CRI: 0.313–0.644) for individuals with failed nests in year t when there was not a flooding event in year t. Dispersal probability was not affected by variation in spring phenology regardless of previous nest fate. Dispersal

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probability was higher for birds with successful nests in years with a major flooding event than years without a major flooding event, and lower for birds with failed nests in years with a major flooding event than years without a major flooding event. Furthermore, dispersal probability for birds with failed nests in years with a major flooding event was lower than those with successful nests in years with a major flooding event. Lastly, fidelity to a nest site increased nest survival by 0.06. Our results suggest that nest-site fidelity for emperor geese follows the WS-LS strategy under certain conditions, but this varies with extreme weather events. We recommend further studies examine the role of individual heterogeneity and habitat quality on nest-site fidelity of geese.

INTRODUCTION

Evolutionary theory predicts that decisions by animals, such as selection of breeding habitat, should ultimately lead to an increase in fitness (Martin 1998, Clark and Shutler 1999, Piper 2011). This is especially true for birds, as their reproductive success is primarily influenced by predation (Ricklefs 1969), and individual decisions on where to nest have the potential to affect exposure of nests to predation (e.g., Martin and Roper 1988, Davis 2005). Fidelity to a breeding site (i.e., nest site) is a common strategy in birds and is believed to be beneficial due to familiarity with local resources and neighbors (Greenwood and Harvey 1982, Anderson et al. 1992), although empirical evidence for demographic benefits of site familiarity is limited (Piper 2011). Whether nest-site fidelity is adaptive often depends on spatiotemporal variation in habitat quality (Switzer 1993). When habitat quality is spatially variable but temporally predictable, dispersal decisions based on reproductive outcome in the previous breeding attempt may be favored (i.e., win-stay lose-shift strategy; WS-LS; Schmidt 2004). The WS-LS strategy suggests that an individual will be more likely to return to the same breeding site if they were previously successful at that site, and more likely to disperse if they were not successful. Alternative strategies, such as fidelity regardless of previous reproductive outcome, may be favored when habitat quality is spatially homogenous but temporally dynamic (i.e., predictability of reproductive outcomes between years is low; Switzer 1993, Gerber et al. 2018).

Nest-site fidelity has been studied extensively in waterfowl (*Anatidae*). Empirical evidence often supports the WS-LS strategy in nest-site fidelity of cavity-nesting waterfowl (Dow and Fredga 1985, Gauthier 1990, Hepp and Kennamer 1992); however, evidence for the WS-LS strategy has been variable in ground-nesting waterfowl, with minimal evidence in some studies (Bustnes and Erikstad 1993, Lecomte et al. 2008) and support in others (Lindberg and Sedinger 1997, Fowler 2005, Öst et al. 2011). Furthermore, observed fitness consequences of nest-site fidelity in waterfowl are variable, and have included greater clutch sizes (Gauthier 1990, Lindberg and Sedinger 1997), earlier nest initiation dates (Hepp and Kennamer 1992, Öst et al. 2011), and higher nest survival (Fowler et al. 2005), with some species exhibiting all of these (e.g., common goldeneyes [*Bucephala clangula*]; Dow and Fredga 1985).

Several studies have examined nest-site fidelity in Arctic-nesting geese, with mixed support for the WS-LS strategy and associated fitness consequences of nest-site fidelity (e.g., Lindberg et al. 1995, Lindberg and Sedinger 1997, Fowler 2005, Lecomte et al. 2008). Timing of nesting in Arctic-nesting geese is complicated by short breeding seasons (Owen 1980), where hatch is timed to coincide with peak forage quality in food plants (Sedinger and Raveling 1986). This often causes annual reproductive phenology to coincide with spring phenology (Ely and Raveling 1984, Petersen 1990). Delayed springs may lead to a longer interval between the time geese arrive on the breeding areas and initiate their nest (Hupp et al. 2006, Hupp et al. 2018), or cause geese to initiate nests while there is still high percent snow cover on the landscape (Petersen 1990). Thus, geese may be faced with tradeoffs between timing of nesting and fidelity to a previous nest site in late springs when previous nest sites may not be available, potentially leading to nest-site dispersal in years of late spring onset (Lecomte et al. 2008). Therefore, progressively earlier springs may enable birds to return to nest sites where they were previously successful. The interplay between environmental conditions and breeding dispersal with its associated fitness consequences is important to understand given rapid environmental change (e.g., Kloskowski 2021).

Longitudinal data on individual animals, particularly using capture-mark-reencounter (CMR) methods, are often used to study dispersal (Bennetts et al. 2009), including nest-site fidelity in birds (e.g., Lindberg and Sedinger 1997). However, investigating nest-site fidelity and associated fitness benefits can be difficult when using CMR data due to imperfect detection and mortality of individuals between breeding attempts (Greenwood and Harvey 1982, Lindberg et al. 1995). To address this dilemma, Lindberg et al. (1995) developed a multistate model to investigate nest-site fidelity of black brant (*Branta bernicla nigricans*), which allowed estimation of dispersal probabilities while accounting for survival and imperfect detection; however, their approach did not address potential causes or fitness consequences of nest-site fidelity. Schaub and von Hirschheydt (2009) developed a modified multistate model to estimate dispersal probability of barn swallows (*Hirundo rustica*) and simultaneously test whether dispersal was influenced by previous experience and whether dispersal led to improved reproductive success, allowing for direct testing of WS-LS strategy and associated fitness benefits of the strategy. While these approaches successfully account for imperfect detection and survival, they did not account for temporary emigration of individuals, which is particularly important for species that forgo breeding (e.g., geese) and can cause bias in parameter estimates when using CMR data (Kendall et al. 1997).

We modified approaches of Lindberg et al. (1995) and Schaub and Von Hirschheydt (2009) to account for temporary emigration, and applied this model to 17 years of CMR data to examine nest-site fidelity of emperor geese (*Anser canagicus*), a species of conservation concern endemic to the Bering Sea region, in which empirical studies of nest-site fidelity are lacking. We predicted that probability of nest-site dispersal would be higher if birds failed their nesting attempt in the previous year (i.e., WS-LS strategy), and returning to the same nest site would lead to higher nest survival due to familiarity with local resources and neighbors. Additionally, we predicted that spring phenology would affect nest-site fidelity in that dispersal probability would be higher in years with relatively later spring due to higher percent snow cover potentially limiting availability of nest sites. Finally, we predicted that dispersal probability would be higher in years following major flooding events due to much lower nest survival in those years (Chapter II) and potential for post-hatch mortality due to the flood.

MATERIALS AND METHODS

Study species and data collection

The emperor goose is a long-lived species endemic to the Bering Sea region (Eisenhauer and Kirkpatrick 1977). Emperor geese nest primarily on the Yukon-Kuskokwim Delta (Y-K Delta) in western Alaska (Eisenhauer and Kirkpatrick 1977), but also less extensively on the Seward Peninsula in western Alaska and in coastal Russia (Schmutz et al. 2020). Emperor geese typically delay breeding until they have reached 3–4 years of age (Schmutz 2000), and often forgo nesting between breeding attempts (Petersen 1992b, Hupp et al. 2006). Our study took place near the Manokinak River (165.10°W, 61.21°N) on the Y-K Delta. The study area is low elevation and flat (<5m above sea level) and interspersed with many small, shallow freshwater ponds and tidal sloughs. Vegetation in the study area consisted primarily of meadows dominated by salt tolerant graminoids (e.g., *Carex ramenskii*) and dwarf-scrub plants (Kincheloe and Stehn 1991, Jorgenson 2000).

We searched 14 contiguous plots (~23 km^2) from 2000–2017 for all emperor goose nests. Timing of initial plot searches was variable among years, but typically took place during late egg laying or early incubation. Once nests were located, we aged eggs using floating (Westerkov 1950) and candling (Weller 1956) and recorded coordinates of nests using handheld GPS receivers. We captured adult female emperor geese on nests using bow net traps (Salyer 1962) and mist nets (Bacon and Ervard 1990), although in some years we captured females during wing molt by herding family groups into corral traps (Owen 1980). These females did not enter our sample until they were encountered on a nest. We banded captured females with a United States Geological Survey (USGS) metal leg band on one leg and a plastic tarsal band engraved with a 3-character alphanumeric code on the other leg. In subsequent years, we resighted marked females on nests using spotting scopes, digital cameras, or physical recaptures on the nest if the plastic tarsal band was worn or missing, or if additional data needed to be collected (e.g., blood samples). We revisited nests at irregular intervals until a fate could be determined (hatched, preyed upon, abandoned, etc.), although crews often left field camps shortly after peak hatch, so not all nests were monitored until hatch in all years. We searched from plots 1994–1998 but did not include these years in analyses due to inconsistent data collection efforts; therefore, emperor geese that were banded prior to 2000 entered our sample on the first occasion they were encountered on a nest between 2000 and 2017.

Statistical analysis

We developed a multistate model with an unobservable state in a Bayesian state space-framework to account for survival, imperfect detection, and temporary emigration when examining nest-site fidelity using CMR data (Kendall and Nichols 2002, Schaub et al. 2004, Bailey et al. 2010). We adapted a similar conceptual model to Schaub and Von Hirchheydt (2009), in which transitions between states in year t and $t+1$ consisted of several “events”, including: (1) the marked bird survived and did not permanently emigrate from the study area between year t and $t+1$ with probability ϕ, (2) the bird returned to the study area, chose to nest, and a nest fate was determined in year $t+1$ with probability π, (3) given the bird returned to the study site and nested, it either returned to the same nest site as year t in $t+1$ or dispersed to a new nest site with probability d, and (4) the bird either nested successfully or failed its nesting attempt in $t+1$ with probability γ if it was observed nesting the previous year, or α if it was not. We calculated Euclidean distances between nest locations in consecutive encounter occasions using nest coordinates. Consistent with Lindberg et al. (1995), we considered movements <200m in consecutive years to be fidelity, while movements ≥200m were considered dispersal. We hypothesized that moving ≥200m would potentially expose nesting females to unfamiliar conditions (i.e., foraging, neighbors), as previous work has reported emperor geese moved a maximum of 195m during incubation breaks (Thompson and Raveling 1987).

To assign states to individuals at encounter occasions, we classified individuals as either “same” or “different” nest site depending on where the individual nested relative to their nest location in the previous encounter occasion, so that transitions between classifications represented nest-site fidelity or dispersal rather than the classification itself (Schaub and von Hirchheydt 2009). Therefore, we classified all individuals as “same” upon initial capture, and based classification in subsequent consecutive encounter occasions on where they nested relative to the previous year, so that transitions from “same” to “same” and “different” to “different” were equivalent and represented fidelity to an individual’s nest site in the previous year, and transitions from “same” to “different” and “different” to “same” were equivalent and represented dispersal to a different nest site than that of the previous year (Schaub and Von Hirchheydt 2009; Equation 1). Because dispersal status was not known if the animal was not detected in the previous year, we classified birds as “same” in year t if they were not encountered in $t-1$. We then classified nest fate at each encounter occasion as either “successful” (≥ 1 egg hatched) or “failed” (no eggs hatched). Therefore, if individuals were encountered in year t, we assigned them to one of four observable states based on combinations of movements from year $t-1$ to year t and nest fate in year t as follows: (1) “same” nest site and successful nest in year t, (2) “different” nest site and successful nest in year t, (3) “same” nest site and failed nest in year t, and (4) “different” nest site failed nest in year t. We also considered an unobservable state (detection probability of 0; Kendall and Nichols 2002, Schaub et al. 2004, Bailey et al. 2010) to account for temporary emigration (e.g., forgoing nesting, temporarily nesting off the study area). We did not include encounter occasions for individuals in which a fate for their nest was not determined because these individuals could not be assigned to a state. Furthermore, observers did not monitor nests until hatch in 2005; therefore, we did not include detections of individuals in 2005 in our analyses.

To fit this model, we constrained parameters so that information was shared among state transitions and parameters were appropriate to test our specific hypotheses. First, we constrained apparent survival probability (ϕ) to be the same for each state, including our observable and unobservable states. We believed this assumption was valid because survival probability is not influenced by previous nest fate in emperor geese (Petersen 1992a), and we had no reason to suspect that dispersal status would influence apparent survival probability. Next, we assumed that dispersal probability (d) from year t to $t+1$ was only dependent on nest fate in year t and not dispersal status (d_H for birds with a successful nest in year t, and d_F for birds with a failed nest). We also assumed that nest survival (γ) in year $t+1$ was only dependent on whether an individual returned or dispersed in year $t+1$ from its nest location in year t (γ_R for birds who returned to the same nest site, and γ_D for birds who dispersed to a new nest site). Thus, we defined our state transition matrix as:

$$\begin{bmatrix} \phi\pi(1-d_H)\gamma_R & \phi\pi d_H\gamma_D & \phi\pi(1-d_H)(1-\gamma_R) & \phi\pi d_H(1-\gamma_D) & \phi(1-\pi) & 1-\phi \\ \phi\pi d_H\gamma_D & \phi\pi(1-d_H)\gamma_R & \phi\pi d_H(1-\gamma_D) & \phi\pi(1-d_H)(1-\gamma_R) & \phi(1-\pi) & 1-\phi \\ \phi\pi(1-d_F)\gamma_R & \phi\pi d_F\gamma_D & \phi\pi(1-d_F)(1-\gamma_R) & \phi\pi d_F(1-\gamma_D) & \phi(1-\pi) & 1-\phi \\ \phi\pi d_F\gamma_D & \phi\pi(1-d_F)\gamma_R & \phi\pi d_F(1-\gamma_D) & \phi\pi(1-d_F)(1-\gamma_R) & \phi(1-\pi) & 1-\phi \\ \phi\pi\alpha & 0 & \phi\pi(1-\alpha) & 0 & \phi(1-\pi) & 1-\phi \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \tag{1}$$

and our observation matrix as:

$$\begin{bmatrix} p & 0 & 0 & 0 & (1-p) \\ 0 & p & 0 & 0 & (1-p) \\ 0 & 0 & p & 0 & (1-p) \\ 0 & 0 & 0 & p & (1-p) \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \tag{2}$$

where p was detection probability, which we assumed was the same for each observable state. This constraint was necessary because detection probability was not identifiable when modeled as a function of reproductive success. We developed our model in the state-space framework following Kéry and Schaub (2012), where we modeled true latent state (z) of individuals (i) at time $t+1$ given their true latent state at time t ($z_{i,t}$), as categorically distributed:

$$z_{i,t+1}|z_{i,t} \sim Categorical(\boldsymbol{\Omega}_{z_{i,t},1\ldots S,i,t}), \tag{3}$$

where $\boldsymbol{\Omega}_{z_{i,t}1\ldots S,i,t}$ was a four-dimensional matrix with the first dimension being the true state at time t, the second dimension being the true state at time $t+1$ given true state at time t (derived from our state transition matrix; S = 6 true states), and the third- and fourth-dimensions being individuals and time, respectively. We modeled the observed state of individual i at time t ($y_{i,t}$) given the individuals true latent state at time t as categorically distributed:

$$y_{i,t}|z_{i,t} \sim Categorical(\boldsymbol{\Theta}_{z_{i,t},1\ldots O,i,t}), \tag{4}$$

where $\boldsymbol{\Theta}_{z_{i,t}1\ldots O,i,t}$ was a four-dimensional matrix with the first dimension being the true state at time t, the second dimension being the observed state at time t given the true state at time t (derived from our observation matrix; O = 5 observed states), and the third- and fourth-dimensions being individuals and time, respectively (Kéry and Schaub 2012). To ensure our model produced unbiased parameter estimates with small sample sizes, we simulated datasets and examined bias and precision of parameter estimates following the workflow of Riecke et al. (2018). We report simulation results and provide simulation code in Supporting Information.

Modeling time structure in multistate models with unobservable states often leads to identifiability problems or biased and imprecise estimates of transition probabilities (Bailey et al. 2010), and limitations in our data set led to poor estimation of dispersal probability with annual random effects, particularly for birds who failed their nesting attempt in year t. Therefore, we only considered a model where parameters were constant except dispersal probability, which we modeled as a function of environmental covariates, and nest survival, which we modeled using an annual random effect as follows:

$$logit(\gamma_{q,t}) = logit\left(\mu_{\gamma_q}\right) + \varepsilon_{\gamma_q,t}, \tag{5}$$

$$\varepsilon_{\gamma_q,t} \sim Normal\left(0, \sigma^2_{\gamma_q}\right), \tag{6}$$

where μ_{γ_q} is the mean nest survival for each dispersal status (q), $\varepsilon_{\gamma_q,t}$ is random annual variation of nest survival for each dispersal status on the logit scale, which we assumed was normally distributed, and $\sigma^2_{\gamma_q}$ is a temporal variance term for each dispersal status.

To examine the influence of environmental conditions on dispersal probability of emperor geese, we included an index of spring phenology in year $t + 1$ and flooding events in year t on the study area as covariates in our model. We developed an index of spring phenology using mean nest initiation dates for each year from the study area. We did not have an estimate of mean nest initiation date from the Manokinak River study site for 2005, therefore we used the mean initiation date from random nest plot surveys on the coastal zone of the Y-K Delta (Fischer et al. 2017), as they were highly correlated with mean initiation dates at the Manokinak River across years (Pearson correlation coefficient [r] = 0.98). Following Kellett and Alisauskas (2019), we calculated early-late indices (ELI) for each year by subtracting the mean initiation date for the entire study period from the mean initiation date for each year. Thus, negative ELI values represented relatively early springs, and positive ELI values represented relatively late springs. To index major floods resulting from extreme weather events (2010 and 2013; Fischer et al. 2010, Fischer and Stehn 2014), we created an indicator variable coded as 0 in years without major flooding events, or 1 in years with major flooding events. We modeled time-specific dispersal probabilities from year t to $t+1$ given nest fate in year t (f) as a linear function of covariates as follows:

$$logit\left(d_{f,t}\right) = \beta_{d_f,0} + \beta_{d_f,ELI} \times ELI_{t+1} + \beta_{d_f,FLOOD} \times FLOOD_t, \qquad (7)$$

where $\beta_{d_f,0}$ is mean dispersal probability in an average spring with no major flooding events on the logit scale, and $\beta_{d_f,ELI}$ and $\beta_{d_f,FLOOD}$ are regression coefficients for ELI and flood years, respectively.

We modeled constant parameters and intercepts on the probability scale with $Uniform(0,1)$ priors and regression coefficients with $Normal(0,100)$ priors. Additionally, we fixed detection probability to 0 in 2005 as plots were not searched that year. To formally test if dispersal probability is higher for birds with successful nests than for birds with failed nests, and if nest survival is higher for birds that returned to the same nest site than those that dispersed, we subtracted posterior samples of d_H from d_F and μ_{γ_D} from μ_{γ_R} to provide predictive posterior distributions of the differences between dispersal probabilities at average spring conditions in years with floods and without floods (Δd), and mean nest survival given dispersal status ($\Delta\mu_{\gamma_q}$). We summarized these distributions by calculating means and the proportions of the distribution on the same side of 0 as the mean (δ), which we interpret as the probability of a difference existing.

We fit our model in JAGS (Plummer 2003) using the “jagsUI” package (Kellner 2021) in R (R Core Team 2022). We summarized posterior distributions of parameters using 3 Markov Chain Monte Carlo (MCMC) chains of 75,000 iterations, where we discarded the first 5,000 iterations as burn in and retained every fifth iteration. We assessed convergence of MCMC chains using $\hat{R}$ values and by inspecting trace plots. We report means and 95% credible intervals (95% CRI) of posterior distributions in results. We also report δ for regression coefficients and interpret it as the probability of a covariate having a positive or negative effect. We interpreted $\delta \geq 0.90$ as strong evidence for a relationship or difference existing, and $0.90 > \delta \geq 0.85$ as moderate evidence.

RESULTS

Our sample consisted of 1,256 encounters of 536 banded emperor geese, in which 279 individuals were resighted or recaptured with a known nest fate a total of 720 times. The number of reencounters per individual ranged from 2 to 11. Of the 720 reencounters with known nest fate, 432 were consecutive reencounters of 201 individuals, with the highest number of consecutive reencounters for an individual being 7. Distributions of distances moved between years t and $t + 1$ for emperor geese with successful nests in year t or failed nests in year t were both skewed (Figure 3-1); therefore, we report the median of distances moved for each group rather than the mean. Median distance moved between years t and $t + 1$ for emperor geese with successful nests in year t was 129.612m (min = 1 m, max = 4235.715m, *n* = 374), while median distance moved for birds with failed nests in year t was 177.722m (min = 3m, max = 1241.145, *n* = 58; Figure 3-1). Mean initiation date from 2001–2017 was 22 May. Early-late index was variable through the study, ranging from -11 in 2016 to 12 in 2012. Nine of the 17 years had ELI > 0, indicating relatively late spring onset, while 8 years had ELI < 0, indicating relatively early spring onset.

Trace plots and $\hat{R}$ values indicated convergence of MCMC chains for our model. Parameter estimates are reported in Table 1. Apparent survival probability of adult female emperor geese across the 17 years of our study was 0.779 (95% CRI: 0.758–0.799; Table 1). The probability of returning to the study area (π) across our study period was 0.484 (95% CRI: 0.451–0.518; Table 1), and detection probability was 0.991 (95% CRI: 0.967–1.00; Table 1).

We found strong support for higher dispersal probability of birds with a failed nest in year t than birds with a successful nest in years without floods in year t ($\Delta d_{no\ flood}$= 0.139, δ = 0.940), suggesting strong evidence for the WS-LS strategy, although estimates of dispersal probability for birds with failed nests in year t were much less precise (Figure 3-2). We did not find support for an effect of spring phenology in year $t + 1$ on dispersal probabilities for birds with successful nests in year t ($\beta_{d_H,ELI} =$ 0.013, 95% CRI: -0.018–0.045, δ = 0.789) and those with failed nests in year t ($\beta_{d_F,ELI}$ = -0.003, 95% CRI: -0.093–0.088, , δ = 0.522). We found strong evidence that dispersal probability for birds with successful nests in year t was higher if there was a flooding event in year t than if there was not a flooding event ($\beta_{d_H,FLOOD}$ = 0.526, 95% CI: -0.034–1.083, δ = 0.967; Figure 3-2), and moderate evidence that dispersal probability for birds with a failed nest in year t was lower if there was a flooding event in year t than if there was not a flooding event ($\beta_{d_F,FLOOD}$ = -0.706, 95% CI: -1.859–0.390, δ = 0.895; Figure 3-2). Importantly, we found moderate evidence that dispersal probability was higher for birds with successful nests in years with a major flooding event in year t than birds with failed nests in years with a major flooding event (Δd_{flood} = 0.145, δ = 0.895; Figure 3-2), contradicting predictions of the WS-LS strategy. Lastly, we found moderate support for higher nest survival in year $t + 1$ if the bird returned to the same nest site as year t than if the bird dispersed ($\Delta\mu_{\gamma_q}$= 0.061, δ = 0.877; Table 1).

DISCUSSION

Previous studies have suggested emperor geese exhibit nest-site fidelity (Eisenhauer and Kirkpatrick 1977, Schmutz and Morse 2000, Hupp et al. 2006), as well as other goose species that nest on the Y-K Delta (Lindberg et al. 1995, Lindberg and Sedinger 1997, Fowler 2005). Our results support these claims under our definition of nest-site fidelity (moving <200m in consecutive years), as our estimates of d_F and d_H suggest that emperor geese are at most just as likely to disperse as they are to return if they fail their nesting attempt in the previous year. The WS-LS strategy suggests that reproductive failure would lead to breeding site dispersal in a subsequent year, which is expected to be adaptive when habitat quality is spatially variable but predictable (Schmidt 2004). We found that emperor geese with successful nests in year t were less likely to disperse ≥200m of their previous nest site in year $t + 1$ than those with failed nests when there was not a major flooding event in year t. We also found that: (1) birds with a failed nest had a slightly higher median dispersal distance the following year than those with a successful nest, and (2) returning to within 200m of an individual's nest site in the previous year led to higher probability of nest survival. These results suggest that dispersal decisions for emperor geese may follow the WS-LS strategy, and that the WS-LS strategy may be adaptive.

While our results support the general pattern of fine-scale nest-site fidelity in emperor geese, we emphasize that our estimates of dispersal probability are conditional on the bird returning to the study area. Specifically, our temporary emigration parameter (π) may account for birds who either returned to within 200m of their previous nest site or dispersed from their previous nest site but their nest was located off the study area so they could not be detected. Our temporary emigration parameter can be thought of as the product of breeding propensity, the probability a bird returns to the study area given it chose to nest, and the probability that observers determine a nest fate given the bird chose to nest and return to the study area; however, it is unclear how much each of these probabilities contribute to our estimate of π. Direct estimates of breeding propensity are difficult to obtain and have not yet been reported for emperor geese. Detection probability for emperor geese from previous studies that did not account for temporary emigration was ~58% for birds marked with tarsal bands, of which breeding propensity was suspected as the primary contributor (Schmutz and Morse 2000). This detection probability is greater than our estimate of π (π = 0.484); however, it does not include the probability of determining a nest fate, although it does include probability of detection given the birds is on the study area. We suspect that breeding propensity and probability of observers determining a nest fate likely contribute most to our estimate of π, but emphasize that temporary dispersal out of the study area likely occurs as well. Therefore, our estimates of dispersal probability may be minimum estimates because birds who dispersed ≥200m and out of the study area were not available for detection in most years given our study design.

The reproductive benefits of nesting early for geese may cause a tradeoff between nesting early and initiating a nest when limited sites are available, which often causes geese to initiate nests at higher percent of snow cover in late springs than early springs (Petersen 1990). Initiating nests at higher percent snow cover in late springs could make dispersal more likely as previous nest sites may not be available (Lecomte et al. 2009). Surprisingly, we found that dispersal probability of emperor geese was unaffected by spring phenology in year $t + 1$, regardless of nest fate in year t. We suspect that low representation of failed nests could have contributed to this result, as precision of our estimates of d_f was poor. Additionally, emperor geese that initiate nests early may nest at sites with higher elevation than those who initiated nests later in years of late spring onset (Petersen 1990), and relative initiation dates for marked emperor geese may be repeatable among years (Petersen 1992b). Therefore, we hypothesize that similar dispersal probabilities between early and late springs may be caused by similar patterns in nest-site selection relative to snow cover due to individual heterogeneity in initiation date, although this hypothesis assumes that individuals selected for similar nest-site characteristics (e.g., elevation) among years, which we were unable to test. Alternatively, emperor geese tend to initiate nests at higher elevation relative to pond levels than randomly selected sites (Petersen 1990), so nest sites simply may not be limited in late springs as higher elevation nest sites often thaw and drain before lower elevation sites. We recommend further studies of nest-site fidelity of geese incorporate individual metrics like initiation date and nest-site characteristics.

Major flooding events on the study area contributed to years of low nest survival for emperor geese in 2010 and 2013 (Chapter II), and led to changes in dispersal probability the following year (Figure 3-2). We found that dispersal probability for birds with successful nests in years with a major flooding event was greater than that for birds with successful nests in years without a major flooding event. We suspect that, although the flooding events may not have caused nest failure for these individuals, it could have caused reproductive failure by flooding recently hatched nests (e.g., within 24 hours of hatch). Additionally, reproductive success of conspecifics could influence dispersal decisions in birds (Doligez et al. 2002, Rioux et al. 2011, but see Citta and Lindberg 2007), which could explain our observed result if successful individuals acquired information regarding poor reproductive success in flooded areas. We were surprised that dispersal probability was lower for females with failed nests in years with a major flooding event than for females with successful nests in years with a major flooding event (Figure 3-2) because this result contradicts predictions of the WS-LS strategy. Flooding events occurred on the mean hatch date in 2013 (29 June), and 5 days prior to mean hatch in 2010 (18 June). Therefore, individuals who failed their nesting attempts were likely close to hatching their nest at the time of the flood (the flood occurred on the predicted hatch date for nests of eight marked individuals in 2013). If the risk of flooding at a given nest site is unpredictable for emperor geese and flooded sites are otherwise high-quality nest sites (e.g., low predation pressure, access to resources), then fidelity to that nest site may be adaptive regardless of whether birds failed due to floods as dispersal may lead to predictable fitness consequences. Previous work on black brant at the Tutakoke River colony on the Y-K Delta reported higher density of nests in the northern portion of the colony that is more prone to flooding than the southern portion that typically exhibits higher predation pressure (Van Dellen and Sedinger 2020), and that individuals are more likely to move to the northern portion of the colony than the southern portion, presumably to escape predation pressure despite risk of flooding (Van Dellen 2016). Thus, we speculate that spatially variable and temporally predictable variation in predation pressure within the study area could explain this result, particularly if predation pressure in flooded areas is low, however we were not able to explicitly test for effects of predation pressure on nest-site fidelity of emperor geese in this study. Additionally, we only had two major flooding events during our study period; therefore, further study is needed to confirm this behavior.

Our results indicate that, although emperor geese generally have >0.50 probability of returning to within 200m of their nest site in the previous year, the decision to return to the same nest site only leads to marginally higher nest survival (~0.06). Similarly, dispersal distance had minimal influence on nest survival of black brant (Lindberg and Sedinger 1997); however, returning to within 150m of a previous nest site led to higher nest survival of cackling geese (*Branta hutchinsii minima*; Fowler

2005). While our results indicate only a slight adaptive benefit of nest-site fidelity in emperor geese, we emphasize that our sample may have been biased towards birds with successful nests. Emperor goose nests have low daily survival probability during egg laying (Petersen 1992b, Chapter II), therefore nests that fail early may not be detected by researchers. Additionally, we suspect that while nest-site fidelity may not lead to substantially higher nest survival, it may lead to other fitness benefits, such as earlier initiation dates or larger clutch sizes (Lindberg and Sedinger 1997), which we did not evaluate due to high rates of nest parasitism in emperor geese (McCloskey 2013).

We parameterized a multistate model to examine nest-site fidelity and associated demographic consequences for a species that often forgoes breeding (Petersen 1992b, Schmutz and Morse 2000), thus is not available for detection each year, and applied this model to a real dataset. While our model provides a framework to examine this question, we were limited in the models we were able to fit due to both modeling constraints (Kendall and Nichols 2002, Schaub et al. 2004, Bailey et al. 2010) and data limitations. While we believe our modeling approach was appropriate to address our questions given our data collection protocol, we emphasize that estimating detection probability separately via the robust design could allow for more complex model structures to be considered (Kendall and Nichols 2002, Bailey et al. 2010), and recommend incorporating that study design and model for studies species that may forgo breeding (e.g., Riecke et al. 2018).

Another limitation of our approach is that it required defining an explicit threshold in which dispersal could be quantified, which is often difficult for ground-nesting birds. Our definition of fidelity (moving <200m in a consecutive nesting occasions) was consistent with Lindberg et al. (1995) for black brant in a similar study system and supported by results of Thompson and Raveling (1987). While we believe our definition of fidelity was appropriate for our species and study system, we suspect that altering this definition would change parameter estimates (e.g., a larger threshold for fidelity would lead to lower dispersal probability). Additionally, like Lindberg et al. (1995), our estimates of dispersal probability rely on individuals being observed and in a definable state in at least two consecutive encounter occasions. Therefore, despite having data over a large temporal scale, precision for some of our parameter estimates was poor.

Using our model, we were able to estimate probability of dispersing ≥200m in year $t+1$ (d) given nest fate in year t, and probability of nest fate in year $t+1$ (γ) given dispersal status in year $t+1$. While we were able to estimate these parameters, few consecutive reencounters of birds who failed their nesting attempt in year t limited the complexity of models that we were able to fit and led to imprecision in estimates of dispersal probability. We suspect that high nest survival of emperor geese (Chapter II) coupled with potential bias inherent in our sampling design may have contributed to our small sample of birds who failed their nesting attempt. Given that we typically captured birds late in incubation or during the brood rearing period, and daily survival probability of nests is low during egg laying (Petersen 1992b, Chapter II), our sample may be biased towards individuals with inherently higher reproductive success. Thus, if there is individual heterogeneity in reproductive success (e.g., Kennamer et al. 2016), then individuals that are more prone to nest failure may simply be underrepresented in our sample. Therefore, we suspect that the differences we observed between dispersal parameters (i.e., d_H and d_F) may be minimum differences, and incorporating methods to sample birds throughout incubation or account for individual heterogeneity while modeling (i.e., Royle 2008) could help further our understanding of population-level patterns and among-individual variance in dispersal decisions of geese.

Using multistate modeling, we were able to demonstrate that nest-site fidelity is a common strategy in emperor geese. While we provide a modeling approach that can account for temporary emigration when examining nest-site fidelity using CMR methods, we recommend further studies of nest-site fidelity in geese that wish to use a multistate modeling approach collect data to supplement detection probability through the robust design, which has been parameterized in JAGS (Riecke et al. 2018) and can be extended to account for multiple states and uncertainty in state assignment (Kendall et al. 2012). Additionally, although we found that dispersal decisions in emperor geese may follow the WS-LS rule under certain conditions, dispersal also seems to be influenced by extreme weather events like flooding. We suspect that individual heterogeneity among individuals may play a significant role in determining dispersal decisions, and recommend it be incorporated into further studies of nest-site fidelity for geese. Lastly, although our results show that nest-site fidelity only leads to marginally higher nest survival, we expect that nest-site fidelity may be adaptive in that it leads to other fitness benefits (e.g., larger clutch size, earlier initiation date), which should be investigated in further analyses.

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FIGURES

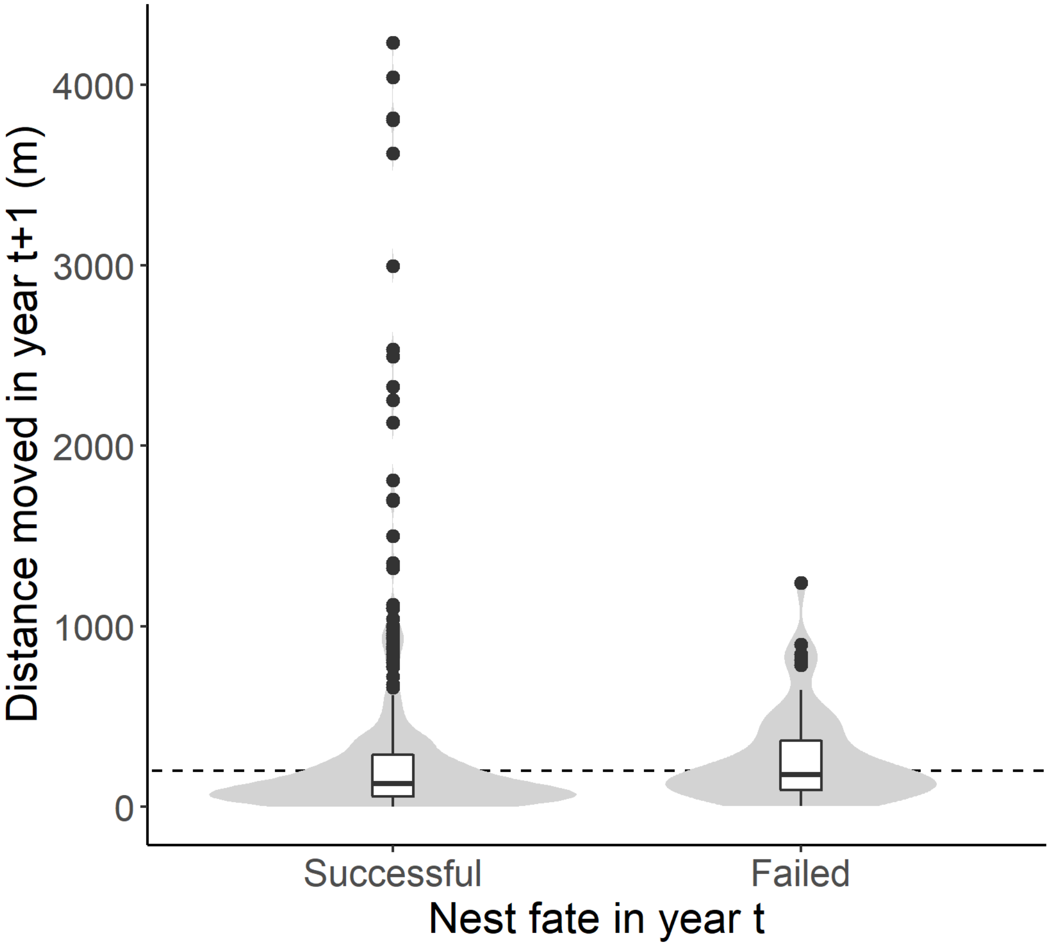

Figure 3-1. Distributions of distances moved between nest locations in year t and $t+1$ geese for those that had a successful nest in year t (*n* = 374). and those that had a failed in year t (*n* = 58). Distances were derived using capture-mark-reencounter data for nesting emperor geese at the Manokinak River, Alaska, USA from 2000–2017. The dashed horizontal line is 200m, which we considered movements <200m as fidelity to a nest site.

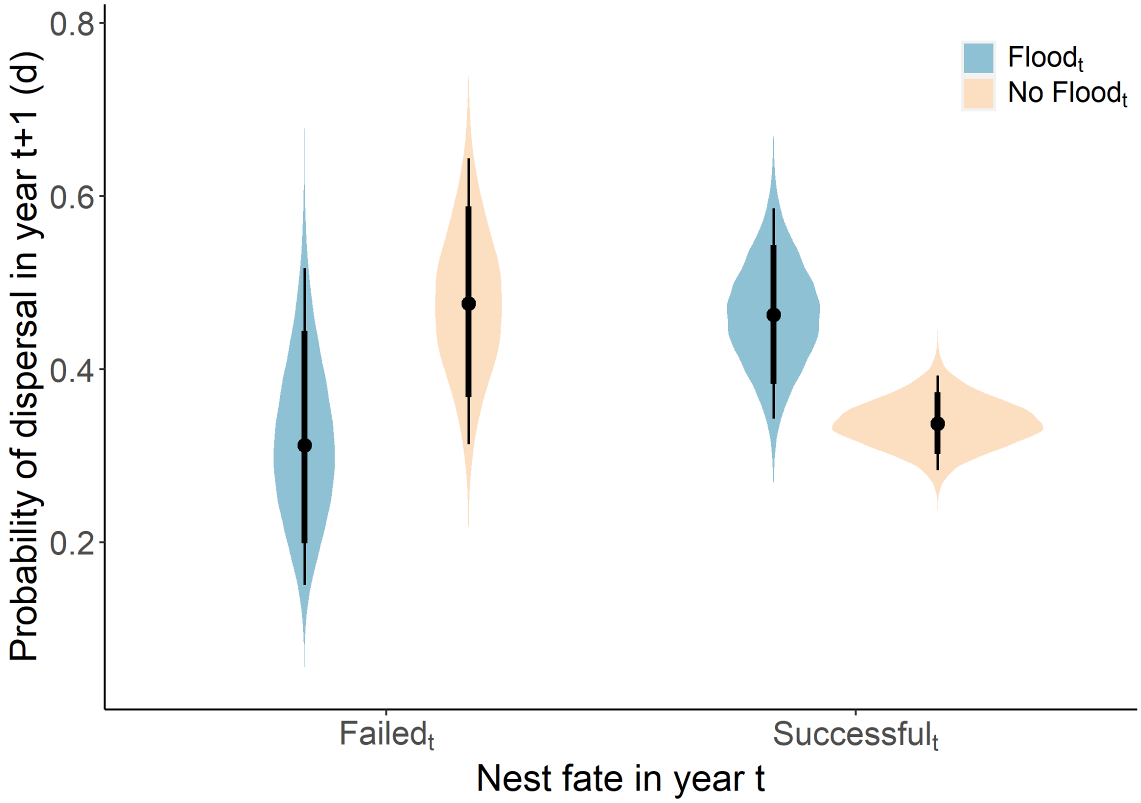

Figure 3-2. Posterior distributions for the probability of nesting emperor geese dispersing ≥200m in year $t + 1$ from their nest location in year t given nest fate in year t and whether there was a major flooding event in year t. Thick lines represent 80% credible limits of posterior distributions, while thin lines represent 95% credible limits. Estimates were derived from a multistate model using capture-mark-reencounter data from the Manokinak River, Alaska, USA from 2000–2017.

TABLES

Table 3-1. Means, standard deviations, and 95% credible intervals (95% CRI) of posterior distributions for apparent survival (ϕ), temporary emigration (π), dispersal (d), nest survival (γ and α), and detection (p) probabilities given previous nest fate (hatched $[H]$ or failed $[F]$) and dispersal status (returned $[R]$ or dispersed $[D]$) from a multistate capture-mark-reencouter model investigating nest-site fidelity of emperor geese at the Manokinak River on the Yukon-Kuskokwim Delta, Alaska, USA from 2000–2017. Parameters with a "." subscript were modeled as constant through the study period, while μ parameters are means from an annual random effect.

Parameter	Mean	SD	95% CI
$\phi_.$	0.779	0.011	0.758–0.799
$\pi_.$	0.484	0.017	0.451–0.518
$d_{H,no\ flood}$[a]	0.337	0.028	0.283–0.393
$d_{F,no\ flood}$[a]	0.477	0.085	0.313–0.644
μ_{γ_q}	0.932	0.034	0.852–0.982
μ_{γ_q}	0.871	0.043	0.779–0.946
$\alpha_.$	0.887	0.019	0.847–0.922
$p_.$[b]	0.991	0.009	0.967–1.000

[a] Estimates are dispersal probability with year t with and no flooding event in year t and average spring phenology in year $t + 1$.

[b] Estimate for 2001–2004 and 2006–2017, as detection probability was fixed to 0 in 2005.

SUPPORTING INFORMATION: Multistate model simulation

We tested the model developed in Chapter III using simulated datasets following the workflow of Riecke et al. (2018). To ensure our model produced unbiased parameter estimates, we simulated 100 populations of individuals captured and released over 20 capture occasions. We simulated the number of animals marked and released in states 1 or 3 within each year as a random Poisson variable with λ = 10. We drew random parameter estimates for each population from uniform distributions with upper and lower limits that were arbitrarily chosen but believed to bound reasonable ranges of parameter estimates for emperor geese (Table S1). We modeled parameters as constant through time with $Uniform(0,1)$ priors. For each simulated population, we summarized posterior distributions for each parameter from one Markov Chain Monte Carlo chain of 15,000 iterations, where we discarded 5,000 iterations as burn in and retained every 5th iteration. We calculated mean bias by subtracting the mean estimate from the simulated value for each simulation and averaged those differences over all simulations. We also calculate the coefficient of variation (CV) for all parameters to evaluate precision of parameter estimates.

Simulation results are reported in Table 3S-1 and Figure 3S-1. All parameters in our model were identifiable under simulated sample sizes. Parameter estimates were unbiased and precise given simulated sample sizes (mean bias <0.01; mean CV <0.2; Figure 3S-1, Table 3S-1).

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Riecke, T. V., A. G. Leach, D. Gibson, and J. S. Sedinger. 2018. Parameterizing the robust design in the BUGS language: lifetime carry-over effects of environmental conditions during growth on a long-lived bird. Methods in Ecology and Evolution 9:2294–2305.

FIGURES

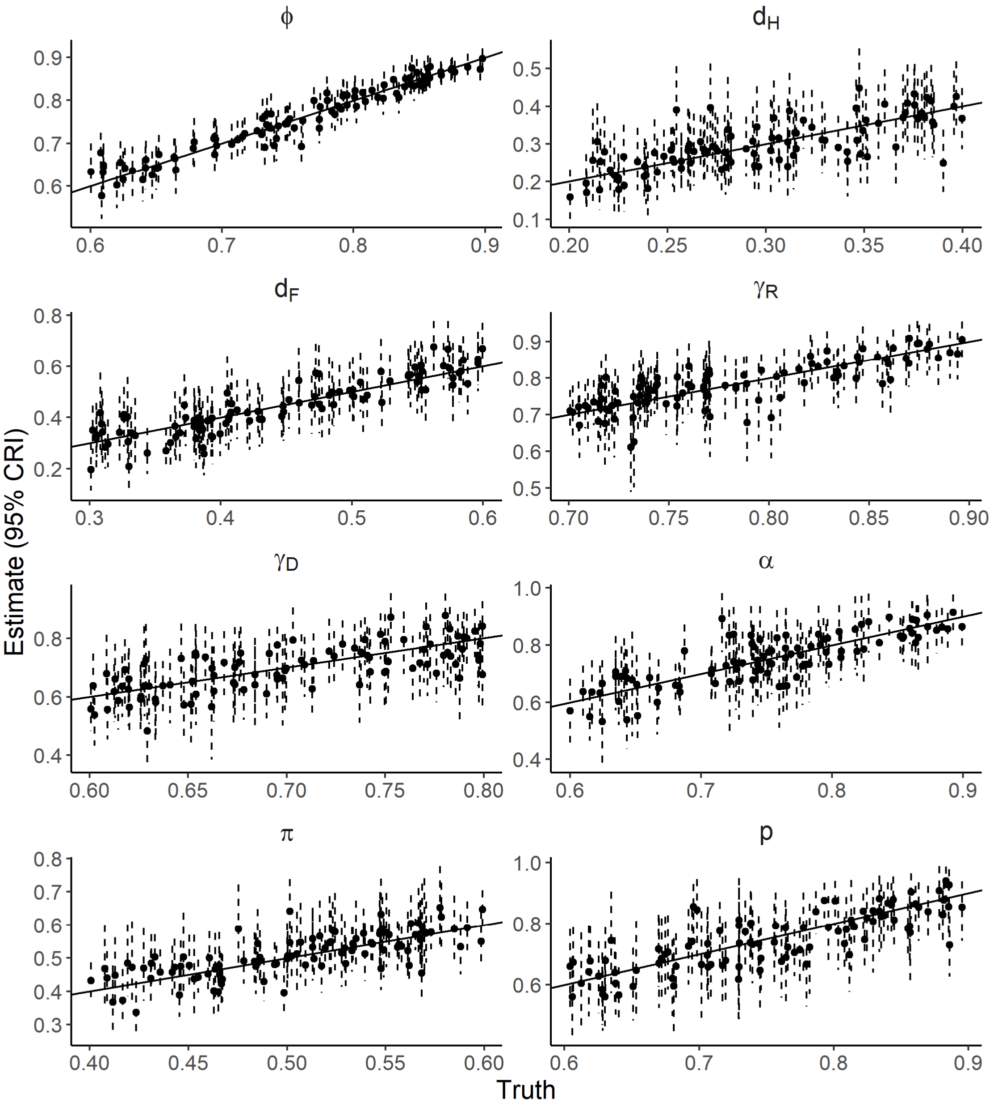

Figure 3S-1. Simulated values (truth) and mean model-based estimates with 95% credible intervals (95% CRI) for each parameter from our multistate model designed to examine nest-site fidelity in the presence of temporary emigration. Our model was fit to 100 simulated populations. Solid line represents perfect alignment between simulated value and estimated value.

TABLES

Table 3S-1. Definitions of parameters, range of simulated values, mean bias, and mean coefficient of variation (CV) for parameters in a modified multistate mark recapture model to examine nest-site fidelity in the presence of temporary emigration.

Parameter	Definition	Simulated range[a]	Mean bias[b]	CV
ϕ_t	Probability of surviving from t to $t+1$ and not permanently emigrating from the study area	(0.6, 0.9)	0.0006	0.028
π_t	Probability of returning to the study area in year $t+1$	(0.4, 0.6)	0.006	0.087
$d_{H,t}$	Probability of moving to a new breeding site in year $t+1$ given successful reproduction in year t	(0.3, 0.6)	0.0006	0.153
$d_{F,t}$	Probability of moving to a new breeding site in year $t+1$ given failed reproduction in year t	(0.5, 0.8)	-0.0009	0.139
$\gamma_{R,t}$	Probability of successfully breeding in year $t+1$ given the animal returns to the same breeding site in year $t+1$ as year t	(0.7, 0.9)	-0.0002	0.050
$\gamma_{D,t}$	Probability of successfully breeding in year $t+1$ given the animal returns to the same breeding site in year $t+1$ as year t	(0.6, 0.8)	-0.003	0.082
α_t	Probability of successfully breeding in year $t+1$ given the animal was not present in the study area in year t	(0.6, 0.9)	-0.001	0.068
p_t	Probability of recapturing the animal in year t given it was present in the study area	(0.6, 0.9)	-0.007	0.080

[a] Range of simulated parameter values drawn from a uniform distribution

[b] Calculated by subtracting estimates from expected and averaging over all simulations

CHAPTER IV. MULTISCALE NEST-SITE SELECTION AND ASSOCIATED FITNESS CONSEQUENCES FOR EMPEROR GEESE ON THE YUKON-KUSKOKWIM DELTA, ALASKA[3]

ABSTRACT

Evolutionary theory predicts that birds select nest sites to maximize reproductive success or survival. We examined how nest-site selection for emperor geese (*Anser canagicus*) on the Yukon-Kuskokwim Delta, Alaska relates to both physical characteristics of nest sites and distance to conspecifics and heterospecifics at two scales: the study area scale and within a 50m radius of a nest (i.e., fine-scale selection). We also examined whether nest-site characteristics led to higher nest survival. We monitored nests of emperor geese on Kigigak Island, Alaska, USA in 2021 and measured characteristics of nest sites both in the field and using a geographic information system. On the study area scale, we found evidence that emperor geese selected nest sites closer to sympatric geese, farther from fox dens with recent sign, and in areas with greater percent cover of water within 50m than what was available. Additionally, we found moderate evidence that emperor geese selected nest sites closer to nests of glaucous gull (*Larus hyperboreus*) than what was available, although they nested ~200m from glaucous gull nests on average. At a fine scale, we found that emperor geese selected nest sites that have lower percent cover of graminoids and are closer to shorelines than what was available within 50m, although there was substantial individual heterogeneity in these relationships. Lastly, we found support for a negative

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[3] Author list includes Thompson, J. M., B. L. Daniels, and B. S. Sedinger.

relationship between daily survival probability of nests and distance to shorelines as well as distance to glaucous gull nests. Our results indicate potential adaptive benefits to nest-site selection, including nesting among predators. We recommend repeated studies over multiple years to examine the benefit that nest sites and predators have on nest survival of geese on the Yukon-Kuskokwim Delta.

INTRODUCTION

Evolutionary theory predicts that birds select nest sites to maximize reproductive success or survival (Hildén 1965, Matin 1998, Clark and Shutler 1999). Thus, selection of nest sites for birds has been a topic of interest to ornithologists as it can have important conservation implications (Davis et al. 2005, Chalfoun and Johnson 2007, Eichholz and Elmberg 2014). Nest survival of birds is most often influenced by predation (Ricklefs 1969); therefore, characteristics of nest sites can influence nest survival by affecting the exposure of a nest to predation. For example, nesting on islands has been shown to increase nest survival for several waterfowl species (Kellett et al. 2003, Miller et al. 2007, Carbaugh et al. 2010) because nesting on islands can seclude nests from terrestrial predators (Larson 1960). Additionally, vertical or lateral concealment of nests by vegetation often leads to higher nest survival (Crabtree et al. 1989, Petersen 1990, Bentzen et al. 2009). While physical characteristics of nest sites often influence nest survival, both presence and density of conspecifics or heterospecifics can increase nest survival through predator swamping (Raveling 1989, Van Dellen and Sedinger 2020), or decrease nest survival by increasing the frequency of aggressive interactions between neighbors (Baldwin et al. 2011). Furthermore, some species may benefit from nesting among avian predators who aggressively defend their nests (Tremblay et al. 1997, Quinn et al. 2003, Quinn and Ueta 2008), although nesting among predators may also increase predation risk on either nests or young, indicating a potential tradeoff (Quinn and Kokorev 2002, Swift et al. 2018).

Broadly, habitat selection is thought to be a hierarchical process, starting from selection of large regions (e.g., range) and ending with selection of specific resources (e.g., food plant; Johnson 1980). In the context of nest-site selection, the orders of habitat selection proposed by Johnson (1980) have been defined as follows: selection of region or latitude (i.e., first order), selection of landscape type within a region (i.e., second order), selection of specific location within a landscape (i.e., third order), and selection of a specific nest site within that location (i.e., fourth order; Eichholz and Elmberg 2014, Kaminski and Elmberg 2014). Thus, the relative importance of various characteristics of nest sites to nest-site selection and their adaptive benefit may be dependent on the scale at which selection is measured (Johnson 1980, Jones 2001, Chalfoun and Martin 2007), emphasizing the importance of defining and modeling nest-site selection at the appropriate scales to match hypotheses and ecology of the species.

The emperor goose (*Anser canagicus*) is a species endemic to coastal Alaska and Russia. Approximately 80–90% of the population nests on the Yukon-Kuskokwim Delta (Y-K Delta) in western Alaska, USA, and they winter along the Alaska Peninsula, the Aleutian Chain, and in coastal Russia (Eisenhauer and Kirkpatrick 1977). No studies have described emperor goose nest sites or examined nest-site selection in relation to physical characteristics and densities of conspecifics and heterospecific geese since the

1990s (Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Petersen 1990). Petersen (1990) examined how physical characteristics of nest sites and distances to conspecific or heterospecific goose nests differ between emperor goose nest sites, cackling goose nest sites, and randomly determined sites on the Y-K Delta from 1982–1986, a period when all goose populations on the Y-K Delta were at their lowest (Fischer et al. 2018). Since their study, populations of cackling geese (cacklers; *Branta hutchinsii minima*) and greater white-fronted geese (white fronts; *Anser albifrons frontalis*) on the Y-K Delta have increased substantially (Fischer et al. 2018), which could have implications for community dynamics as they relate to nest survival.

We examined nest-site selection for emperor geese at two scales: selection of a location within the study area and fine-scale selection of a nest site (analogous to 3rd and 4th order selection, respectively; Johnson 1980, Eichholz and Elmberg 2014, Kaminski and Elmberg 2014) on Kigigak Island, Alaska, USA. We also examined how nest-site characteristics at both scales affected nest survival of emperor geese. At the study area scale, we predicted that emperor geese would select to nest in areas with greater percent cover of water within 50m of the nest, farther from potential predators (glaucous gulls [*Larus hyperboreus*] and Arctic foxes [*Alopex lagopus*]; Eisenhauer and Kirkpatrick 1977), and closer to conspecific and heterospecific geese (cacklers and white fronts). Accordingly, we predicted that nesting in areas with more water within 50m of the nest may lead to higher nest survival as complex shorelines may reduce detection of emperor goose nests to predators (Lecomte et al. 2008) and reduce distances traveled during incubation breaks to obtain water (Lecomte et al. 2009). Additionally, we predicted that nesting farther away from predators would reduce predation risk for emperor geese, and nesting closer to heterospecific geese would lower predation risk for emperor geese because heterospecific geese like cacklers are less efficient at defending their nest against foxes than emperor geese (Mickelson 1975). At a fine scale, we predicted that emperor geese would select nest sites with greater percent cover of graminoids and dwarf shrubs, and nests that are closer to shorelines of ponds and sloughs. We predicted that more graminoids would help conceal emperor goose nests from predators, thus leading to higher nest survival (Petersen 1990). Additionally, we predicted that nesting at sites with greater percent cover of dwarf shrubs may lead to higher nest survival because dwarf shrubs typically occur at higher elevations on the Y-K Delta (Jorgenson 2000) which may enhance the female's view of their surroundings (Petersen 1990, Stickney et al. 2002), allowing for early detection of predators.

METHODS

We collected data on Kigigak Island (60°50'N, 165°50'W; Figure 4-1) on the Y-K Delta in western Alaska. Kigigak Island is ~32.5 km^2 and is located at the mouth of the Ninglick River on the Bering Sea coast of the Y-K Delta. Kigigak Island has an elevation of 1–4m above sea level and holds many small and shallow ponds, lakes, tidally influenced sloughs, and expansive tidal mudflats around its border (Solovyeva et al. 2017). The dominant broad vegetation communities are low coastal graminoid meadow and upland moss-lichen tundra (Moran 2000, Solovyeva et al. 2017). Kigigak Island supports a high diversity and abundance of nesting water birds, including black brant (*Branta bernicla* *nigricans*), cacklers, white fronts, spectacled eiders (*Somateria fischeri*), and common eiders (*Somateria mollisima*; Moran 2000, Saalfeld et al. 2017).

In 2021, we searched seven 1.14 X 0.62km contiguous plots and an additional .13 km^2 area adjacent to the plots and bounded by a major tidal slough (Figure 4-1) for all emperor goose, cackler, and white-front nests. These plots are consistent with monitoring efforts for emperors on Kigigak since 2017 (Daniels 2018). We systematically searched plots for nests by walking along boundaries of ponds and sloughs and walking transects through meadows. We identified species of nests by observing females flushing from nests or examining down and contour feathers within the nest when a female was not observed. Once we located a nest, we recorded coordinates using handheld GPS receivers (± 3.65m; Garmin, Olathe, KS). We recorded the number of eggs in the nest bowl and determined age of the nest by floating (Westerkov 1950) and candling (Weller 1956) 3 eggs. After initial visits, we revisited emperor goose nests at irregular intervals until a fate could be determined (hatched, predated, abandoned). We considered a nest successful if we found eggshell fragments with detached egg membranes in the nest. We only revisited nests of cacklers and white fronts opportunistically and did not determine fates for most of their nests. As part of an ongoing mark-resight study, we trapped female emperor geese on the nest using bow-net traps (Salyer 1962) within the last 5 days of incubation (Daniels 2018).

While searching plots, we also recorded coordinates for glaucous gulls (*Larus hyperboreus*) nests and Arctic fox (*Alopex lagopus*) dens. When visiting Arctic fox dens, we recorded whether a fox was observed at the den or if there was recent sign of fox near the den (scat, hair, prey carcasses, etc.), and only included those with recent sign in analyses. We did not confirm if dens were active but assumed dens with recent sign were used by foxes during the nesting season in some capacity and may indicate an area of higher fox predation pressure.

Study area scale nest-site selection

To examine selection of nest sites at the study area scale, we imported locations of emperor goose, cackler, white-front, and glaucous gull nests into a geographic information system using ArcGIS Pro (Esri, Redlands, CA, USA). We generated 5 random points (available) for each nest site (used) within the boundaries of the study area and only in areas that were able to hold a nest (i.e., not over water or mud). We manually digitized boundaries of water bodies in the study area using 50cm resolution Maxar satellite imagery available through ArcGIS Pro (Esri 2022) for inclusion in analyses. We considered the boundary of waterbodies to be the maximum water line, and only considered water bodies that contained water at the time the imagery was collected (6 June 2014); therefore, dried ponds were not included. Additionally, we digitized boundaries of patches of upland moss-lichen tundra, which were located using previously mentioned satellite imagery and a digital elevation model for the Y-K Delta created from LiDAR data collected in 2016 (NOAA OCM Partners 2022). For each nest and random point, we measured the distance to nearest emperor goose nest (m), distance to nearest cackler or white front nest (m), distance to nearest glaucous gull nest (m), distance to nearest fox den with active sign (m), percent cover of water within 50m, and distance to nearest upland (m) using ArcGIS Pro. We considered percent cover of water within 50m of the nest because emperor geese on average moved ~50m from their nest during incubation breaks, therefore may select for nest-site characteristics at that scale (Thompson and Raveling 1987). We considered nests and random points that were located within upland patches to be 0m from the nearest upland.

To examine nest-site selection at the study area scale, we modeled the response (Y_i; 1 for nest site, 0 for available site) for each site (i) as a Bernoulli process:

$$Y_i \sim Bernoulli(p_i). \tag{1}$$

where we modeled success probability (p_i) as a linear function of predictor variables as follows:

$$logit(p_i) = \alpha + \sum \beta_x \boldsymbol{X}_{i,x}, \tag{2}$$

where α is the intercept on the logit scale, β_x is a vector of regression coefficients for each covariate (6; Table 1), and $\boldsymbol{X}_{i,x}$ is a matrix of x = 6 predictor variables (Table 4-1) for each used or available site (i). We z-standardized predictor variables before including them in the model. We modeled the intercept on the logit scale and regression coefficients with $Normal(0{,}100)$ priors. For each regression coefficient, we calculated the proportion of posterior samples with the same sign as the mean (f), and interpret f as the probability of a positive or negative relationship existing. We interpreted coefficients with $f \geq 0.90$ as having strong evidence for a relationship, and coefficients with $0.90 > f \geq 0.85$ as having moderate evidence for a relationship. We fit our model in JAGS (Plummer 2003) through the “jagsUI” package (Kellner 2021) in R (R Core Team 2022). We sampled 3 Markov Chain Monte Carlo (MCMC) chains of 25,000 iterations, where we discarded the first 1,000 iterations as burn-in and retained every fifth iteration. We present means, 95% credible intervals (95% CRI), and f for posterior distributions of all models.

Fine-scale nest-site selection

We considered fine-scale nest-site selection as the selection of a specific nest site within a 50m radius, consistent with the average distance traveled by emperor geese during incubation breaks (Thompson and Raveling 1987). We measured a variety of vegetative characteristics at each nest site and two randomly determined points per nest located within 50m of the nest site. Due to time constraints, random points were only measured for a random sample of approximately half of the nests in each of the 7 plots. We randomly determined a distance and azimuth of random points from the nest site in the field using a random number table. To avoid biases associated with collecting measurements at nests on the day a fate was determined (Gibson et al. 2016, Ringelman and Skaggs 2019), we attempted to collect measurements on or after the predicted hatch date for each nest. Thus, measurements were collected on average 5.93 days after predicted hatch (SD = 2.92) and ranged from the predicted hatch date to 17 days after the predicted hatch date. We measured percent cover of vegetation types using two 50 X 50cm quadrats placed 25cm north and south of the center of the nest bowl. Quadrats were placed either east or west when north or south were unavailable (i.e., in a pond or on a mudflat). We separately estimated percent cover to the nearest 5% of grasses, sedges, forbs, and dwarf shrub species (i.e., *Salix* spp., *Empetrum nigrum, Rubus chamaemorus*); therefore, percent cover of vegetation types did not need to sum to 100%. We also measured trace amounts of a plant (1% cover). We summed percent cover for grasses and sedges (both live and dead; % cover of graminoids) and dwarf shrub species (% cover of shrubs) and averaged those across both north and south quadrats for inclusion as variables in nest-site selection analyses. We used GPS points from nests and random sites sampled in the field to measure distances (m) from nests and random points to the nearest shoreline in ArcGIS Pro. Due to GPS error, some nests and random points were located within pond polygons; we assumed those nests were on the edge of the pond and assigned the distance from shoreline as 0m. One nest was removed from this analysis because a random site was >75m from a nest site, indicating a potential error in recording coordinates.

We fit a hierarchical discrete choice model to examine fine-scale nest-site selection (Cooper and Millspaugh 1999, Manly et al. 2002, Harju et al. 2011). We defined a choice set (i) as each nest site and the 2 randomly determined sites within 50m of the nest (j). We modeled the response for each choice set ($U_{i,1:J}$; 1 for used sites, 0 for available sites) as multinomially distributed:

$$U_{i,1:J} \sim Multinomial\left(q_{i,1:J}, 1\right), \tag{3}$$

$$q_{i,j} = \frac{e^{(\Sigma \beta_{i,x} x_{i,j,x})}}{\sum_j e^{(\Sigma \beta_{i,x} x_{i,j,x})}}, \tag{4}$$

where $q_{i,j}$ is the relative probability that the j^{th} site in the i^{th} choice set was selected, J is the number of sites within each choice set (J = 3; 1 used and 2 available sites), $\beta_{i,x}$ is a vector of choice-set-specific regression coefficients for each predictor variable (3; Table

4-1), and $\boldsymbol{X}_{i,j,x}$ is a matrix of x = 3 predictor variables corresponding to each regression coefficient for each site within each choice set. We z-standardized predictor variables before including them in the model. Because availability of resources likely varies among choice sets, we modeled regression coefficients for each choice set as random variables as follows:

$$\beta_{i,x} \sim Normal(\mu_{\beta_x}, \sigma_{\beta_x}^2), \tag{5}$$

where μ_{β_x} and $\sigma_{\beta_x}^2$ are the population-level mean regression coefficient for predictor variable x and associated variance, respectively (Harju et al. 2011, Specht et al. 2018). We based inference from the population-level mean coefficient for each predictor variable and interpreted the standard deviation (σ_{β_x}) as the amount of individual heterogeneity among choice sets. We modeled population-level mean regression coefficients with $Normal(0,100)$ priors, and standard deviations with $Uniform(0,10)$ priors. We fit our model in JAGS (Plummer 2003) through the “jagsUI” package (Kellner 2021) in R (R Core Team 2022). We sampled 3 MCMC chains of 80,000 iterations, where we discarded the first 5,000 iterations as burn-in and retained every tenth iteration.

Influence of nest-site characteristics on nest survival

We fit a nest survival model using predictor variables included in both resource selection models to examine if nest-site characteristics were adaptive in that they led to higher nest survival (Table 4-1). Additionally, we included a measure of visual obscuration for nests, which we measured in the field using a Robel pole (Robel et al. 1970, Toledo et al. 2008) with 10 cm graduations. We placed the Robel pole immediately north of the nest and measured visual obscuration as the number of bands (to the nearest half band) totally obscured by vegetation by viewing the pole from 4m away at 1m height from all four cardinal directions (Robel et al. 1970). Some nests and random sites were located directly on the shore of deep ponds, which prevented us from measuring visual obscuration from the direction of the pond. Therefore, we calculated visual obscuration scores by averaging all available visual obscuration measurements for each nest or random site. We only included nests in which all measurements were available in this analysis (*n* = 221).

We generated encounter histories for each nest using the first day the nest was found (I), the last day the nest was seen active (J), the last day the nest was checked (K), and nest fate (successful or failed). For successful nests, J = K and is the estimated or observed hatch date, and for failed nests K is the predicted hatch date if nests were found failed after their predicted hatch (Dinsmore et al. 2002). We modeled period survival (S; S = 1 for nests that survived the period, S = 0 for nests that failed during the period) for the interval from I to $J-1$ and from J to $K-1$ for each individual nest (i) as Bernoulli processes with the success probability equal to the product of a vector of daily survival probabilities (DSPs) for each nest (i) and day (j) combination as follows:

$$S_i^{I,J-1} \sim Bernoulli(\textstyle\prod_I^{J-1} DSP_{i,j}), \tag{6}$$

$$S_i^{J,K-1} \sim Bernoulli(\textstyle\prod_J^{K-1} DSP_{i,j}). \tag{7}$$

We modeled variation in DSP for each combination of nest and day as a linear function of predictor variables as follows:

$$logit\left(DSP_{i,j,t}\right) = \alpha + \sum \beta_x \boldsymbol{X}_{i,j,x}, \tag{8}$$

where α is mean DSP on the logit scale, β_x is a vector of regression coefficients for each predictor variable (Table 4-1), $\boldsymbol{X}_{i,j,x}$ is a matrix of x = 10 predictor variables for each nest and day combination. We tested for collinearity between predictor variables by calculating Pearson correlation coefficients (r < 0.55 for all predictor variables). We z-standardized nest-site predictor variables before including them in the model. To control for potential effects of trapping, we also included an indicator variable (coded as 0 or 1) for the day a female was trapped on the nest, as this has been previously shown to negatively affect daily survival probability of emperor goose nests (Chapter II). We modeled mean DSP on the probability scale with a $Uniform(0,1)$ prior, and modeled regression coefficients with $Normal(0,100)$ priors. We fit our model in JAGS (Plummer 2003) through the jagsUI package (Kellner 2021) in R (R Core Team 2022). We sampled 3 MCMC chains of 50,000 iterations, where we discarded the first 5,000 iterations as burn-in and retained every tenth iteration.

RESULTS

A total of 225 emperor goose nests, 568 cackler nests, 121 white-front nests, and 126 glaucous gull nests were found in the study area on Kigigak Island in 2021. Of those 225 emperor goose nests, 221 had vegetation characteristics measured at the nest site, and 121 had vegetation characteristics measured at randomly determined points within 50m of the nest site (*n* = 242 random points). Additionally, 12 fox dens were located, 10 of which had recent sign and were included in analyses.

Our study area scale nest-site selection analysis consisted of all 225 emperor goose nests monitored in the study area in 2021, and 1,125 random points. We found strong evidence that relative probability of use was negatively related to distance to the nearest cackler or white front nest (f = 0.973; Figure 4-2A and 3B) and positively related to percent cover of water within 50m of the site (f = 1.000; Figure 4-2A and 3A) and distance to the nearest fox den with recent sign (f = 0.935; Figure 4-2A and 3C). Additionally, we found moderate evidence that relative probability of use was negatively related to distance to the nearest glaucous gull nest (f = 0.886; Figure 4-2A and 3D). We did not find evidence that emperor geese selected to nest closer to nests of other emperor geese (f = 0.824) or farther from uplands (f = 0.775; Figure 4-2A).

Our discrete choice nest-site selection analysis found strong evidence that relative probability of use was negatively related to percent cover of graminoids near the nest at the population level (f = 0.999, Figure 4-2B), although there was substantial heterogeneity in the relationship among individual choice sets ($\sigma_{\beta_{graminoid}}$ = 1.059, 95% CRI: 0.054–2.726). Additionally, we found strong evidence that relative probability of use was negatively related to distance to the nearest shoreline at the population level (f = 0.995, Figure 4-2B), although there was also substantial heterogeneity among individual choice sets ($\sigma_{\beta_{shoreline}}$ = 0.681, 95% CRI: 0.021–2.190). We did not find evidence that emperor geese selected nests with greater percent cover of dwarf shrubs (f = 0.702).

Our nest survival analysis consisted of those 221 nests that had all nest site measurements. Daily survival probability of nests with all other covariates held constant at their mean was 0.998 (95% CRI: 0.996–0.999). We found strong evidence for a negative effect of trapping on DSP (β_{trap} = -3.157, 95% CRI: -4.289–-1.848, f = 1.000), in that trapping a female on the nest lowered DSP to 0.941 (95% CRI: 0.872 – 0.985) for that day, with all other variables held constant at their mean. We found strong evidence that distance to glaucous gull nest (f = 0.906) and distance to shoreline (f = 0.948) were negatively related to DSP (Figure 4-4), in that nests located near gull nests or shorelines had higher DSP, and DSP declined with distance from gull nests or shorelines (Figure 4-5). We did not find evidence that distance to nearest conspecific goose nest (f = 0.574), distance to nearest heterospecific goose nest (f = 0.779), distance to nearest fox den with recent sign (f = 0.532), distance to nearest upland (f = 0.637), percent cover of water within 50m of the nest (f = 0.704), percent cover of graminoids near the nest (f = 0.757), percent cover of dwarf shrubs near the nest (f = 0.587), and visual obscuration of nests (f = 0.603) affected daily survival probability (Figure 4-4).

DISCUSSION

Nest-site selection of emperor geese has previously been described by Mickelson (1975) and Eisenhauer and Kirkpatrick (1977), and quantified by Petersen (1990); however, our study is the first to consider nest-site selection in a scale-specific context, which provides new insights to important relationships. Additionally, our study provides a contemporary analysis of the relationships between nest-site characteristics and nest-site selection and subsequent nest survival, which may have changed since previous studies due to vegetation and avian community shifts (e.g., Fischer et al. 2018, Jorgenson et al. 2018).

On the study area scale, we found that emperor geese select nest sites with greater percent cover of water within 50m of the nest. This is consistent with descriptions from Eisenhauer and Kirkpatrick (1977) and Mickelson (1975), who reported that nest sites were mostly located on shorelines or grass/sedge flats near water. Thus, our results provide quantitative evidence that emperor geese may avoid expansive meadows with few water bodies, which are relatively uncommon in our study area but held the fewest emperor goose nests. It is possible that differences in detection probability of nests between meadows and areas with greater percent cover of water could contribute to this result; however, we believe that potential differences in detection were minimal because observers searched meadows thoroughly and emperor goose nests are conspicuous. At the fine scale, emperor geese selected nest sites that were closer to shorelines. Accordingly, our results indicate an adaptive benefit to nesting near water, as distance to shorelines was negatively related to DSP of nests (Figure 4-5A). Nesting in areas with more water could reduce foraging efficiency of foxes (Lecomte et al. 2008) and reduce distances that females need to travel to obtain water or preen and bathe during incubation breaks, thus reducing the amount of time a nest is unattended and exposed to predation (Lecomte et al. 2009). Although we observed higher nest survival for birds nesting closer to water, fitness benefits may be more pronounced in years with lower abundance of alternative prey (i.e., microtines; Stickney 1991, Lecomte et al. 2008) than was anecdotally observed on Kigigak Island in 2021.

Additionally, nesting near ponds or sloughs with tidal influence may increase risk of flooding during extreme weather events, as nests located directly adjacent to tidal ponds were nearly flooded during high tides in 2021 (Thompson, J. M., *personal observation*). Thus, we emphasize that a thorough understanding of the fitness benefits of nest-site selection requires further study on a larger temporal scale.

Graminoids are a food source for emperor geese once they arrive at the nesting grounds (Eisenhauer and Kirkpatrick 1977). Additionally, they may provide vertical or horizontal cover to unattended nests (Petersen 1990). Therefore, we were surprised that emperor geese selected areas with lower percent cover of graminoids on a small scale, although the relationship between relative probability of use and percent cover of graminoids was variable among individuals. Dead graminoids are often the primary plant used as nest material for emperor geese (Eisenhauer and Kirkpatrick 1977), and although we attempted to measure percent cover of graminoids in areas where minimal graminoids were removed by geese for construction of nest bowls (25cm from the center of the nest bowl), we cannot be certain that removal of graminoids by females prior to nesting did not cause this result.

Petersen (1990) found that emperor geese select nest sites with a greater percent cover of dwarf shrubs than random sites, although our results did not support this. Dwarf shrubs on the Y-K Delta (e.g., *Salix* spp., *Empetrum nigrum*) typically occur at slightly higher elevations than vegetation communities dominated by graminoids (Jorgenson 2000), thus may become available before some graminoid meadows in the spring and can help enhance a female's view of their surroundings when incubating

(Stickney et al. 2002). Dwarf shrubs only occurred in ~50% of the choice sets we sampled; therefore, we suspect that selection (or avoidance) of vegetation communities that have dwarf shrubs may occur at the study area scale, which we did not measure in our study. If selecting to nest in vegetation communities that are at higher elevation is due to earlier availability of these sites in spring, then perhaps individuals who consistently nest earlier relative to others (Petersen 1992) repeatedly select nest sites in these communities. Studies to examine if individual emperor geese consistently chose nests with similar characteristics among years could help further our understanding the role of individual heterogeneity and environmental variation in shaping individual decisions and their associated fitness benefits.

Previous work on nest-site selection of emperor geese suggest that they do not nest closer to nests of conspecific or heterospecific geese than expected by chance when random sites were located within 15m of nests (Petersen 1990); however, we found that emperor geese selected nest sites closer to heterospecific geese when selection was measured at the study area scale (Figure 4-3B). Despite this finding, it is unclear from our results whether emperor geese selected to nest near heterospecific geese. Emperor geese generally nest earlier than cacklers (~2 days on average, Fischer et al. 2017), which were the most abundant heterospecific goose on Kigigak Island in 2021. Therefore, we speculate that this result may simply be due to selection of the same broad habitat types. Additionally, while emperor geese nested closer to heterospecific geese than what was available, our results did not indicate that nesting closer to heterospecific geese was adaptive in that it led to higher nest survival. This was contrary to our prediction that higher densities of nests, particularly cacklers who are less efficient at defending their nests against predators than emperor geese (Mickelson 1975), may lead to lower predation rates on emperor nests. Abundance of voles on Kigigak was significantly greater in 2021 than previous years (Thompson, J. M., *personal observation*), which could have buffered predation on emperor goose nests because more voles are consumed by Arctic foxes in years of high vole abundance (Stickney 1991). Additionally, if foxes focus foraging efforts on areas with higher density of nests (Stickney 1991), then emperor geese that nest further away from sympatric geese may simply be in areas with lower predation pressure from foxes, potentially equalizing nest survival across distances from sympatric geese.

Nesting in close association with predators has been shown to have adaptive benefits for some species of geese (Tremblay et al. 1997, Quinn et al. 2003). We found that emperor geese nested closer to glaucous gull nests than what was available, although we do not interpret that to mean that emperor geese select to nest within glaucous gull colonies because they nested ~200m on average from the nearest glaucous gull nest (Table 4-1). We suspect that this result may simply be due to similar habitat selection (i.e., avoiding expansive meadows), although our results indicate higher nest survival for birds nesting closer to glaucous gull nests, suggesting a fitness benefit to nesting near glaucous gulls (Figure 4-5B). While glaucous gulls prey upon goose eggs, eggs are not a major part of their diet during the breeding season (Schmutz and Hobson 1998); however, emperor goose goslings are often consumed by glaucous gulls (Schmutz et al. 2001, Bowman et al. 2004). Therefore, our results may suggest a tradeoff associated with nesting among glaucous gulls, but simultaneous investigations of nest and brood predation for nests near and far from glaucous gull colonies are needed to formally test this. We also found that emperor geese selected nest sites farther from active fox dens, suggesting they may avoid areas with known fox presence. However, high predation rates of emperor goose nests near dens prior to nest searching could potentially explain this result, warranting cautious interpretation.

While we provided an in-depth examination of nest-site selection and nest survival for emperor geese, we emphasize that there were several limitations to our study. First, we only collected data during one breeding season, which prohibited us from examining interannual trends in habitat associations and nest survival. Given relatively high vole abundance in 2021 (Thompson, J. M., *personal observation*) and high nest abundance in 2021 compared to other years of the study (Daniels 2018), we suspect that predation of nests may have been lower than normal. Therefore, relationships between nest-site characteristics and nest survival may have been obscured. Second, we only considered nests found on Kigigak Island. Based on predictive modeling of waterbird nest densities related to broad-scale habitat characteristics, Kigigak Island is predicted to have relatively high densities of most goose species on the Y-K Delta (Saalfeld et al. 2017). Therefore, Kigigak Island may represent ideal habitat and unusual nest densities that may not be representative of the rest of the Y-K Delta. Lastly, while we found some evidence for adaptive nest-site selection, we emphasize that we only considered higher nest survival as a fitness consequence. Nest sites can influence other demographic parameters such as survival of incubating females

(Miller et al. 2007). Furthermore, nesting closer to brood rearing areas can affect growth or survival of goslings (Mainguy et al. 2006). Long-term comparative studies of nesting habitat selection and associated fitness consequences for multiple demographic rates across multiple sites can help to further understand habitat selection and associated fitness consequences for emperor geese on the Y-K Delta.

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FIGURES

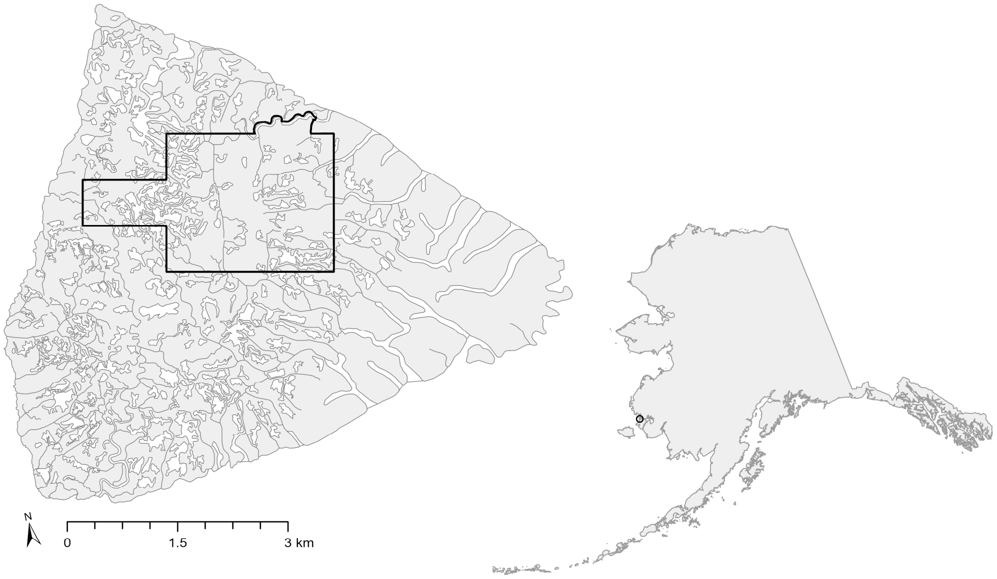

Figure 4-1. Location of Kigigak Island on the Yukon-Kuskokwim Delta, Alaska, USA, and boundaries of the study area where emperor goose nests were monitored in 2021.

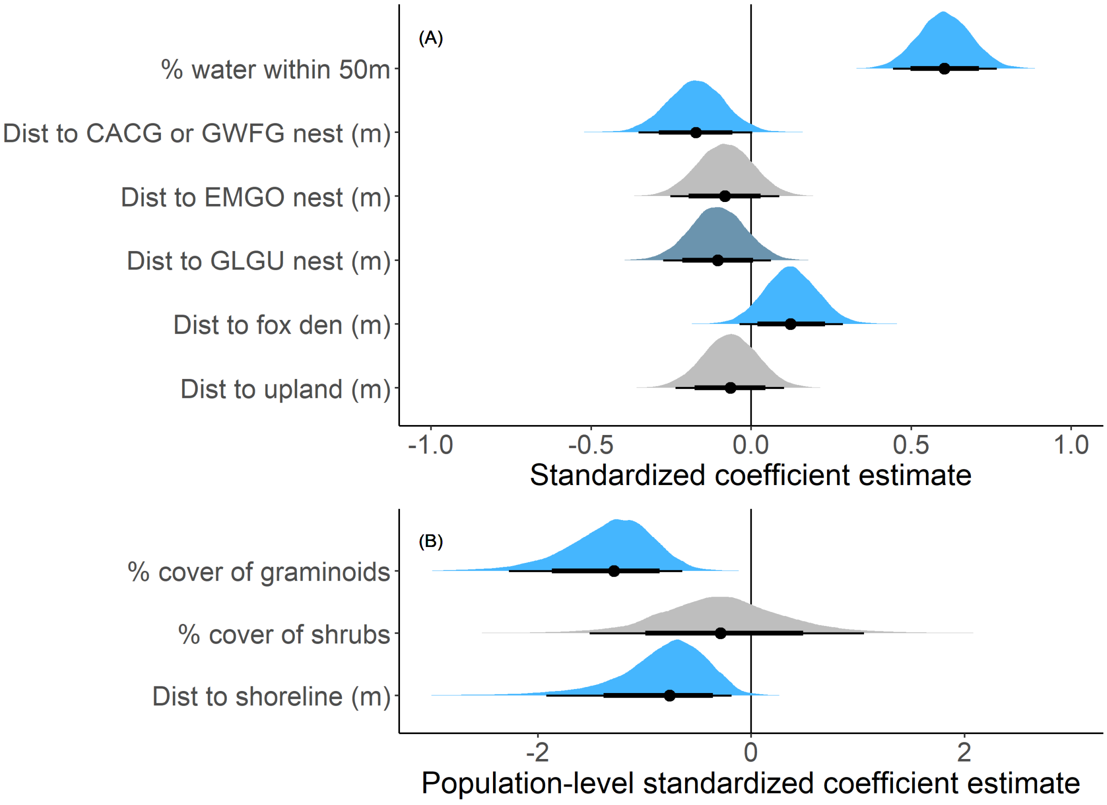

Figure 4-2. Posterior distributions of regression coefficients from our (A) logistic nest-site selection model examining study area scale selection, and (B) discrete choice model examining fine-scale selection for emperor goose nests located in 2021 on Kigigak Island, Alaska, USA. Coefficient estimates from our discrete choice model (B) are means from a random slope term. Thin lines are 95% credible limits, and thick lines are 80% credible limits. Distributions shaded in light blue had strong support for an effect ($f \geq 0.90$), distributions shaded in dark blue had moderate support for an effect ($0.90 > f \geq 0.85$), and distributions shaded in grey had weak or no support for an effect ($f < 0.85$). Abbreviations are those used by the U.S. Geological Survey Bird Banding Laboratory.

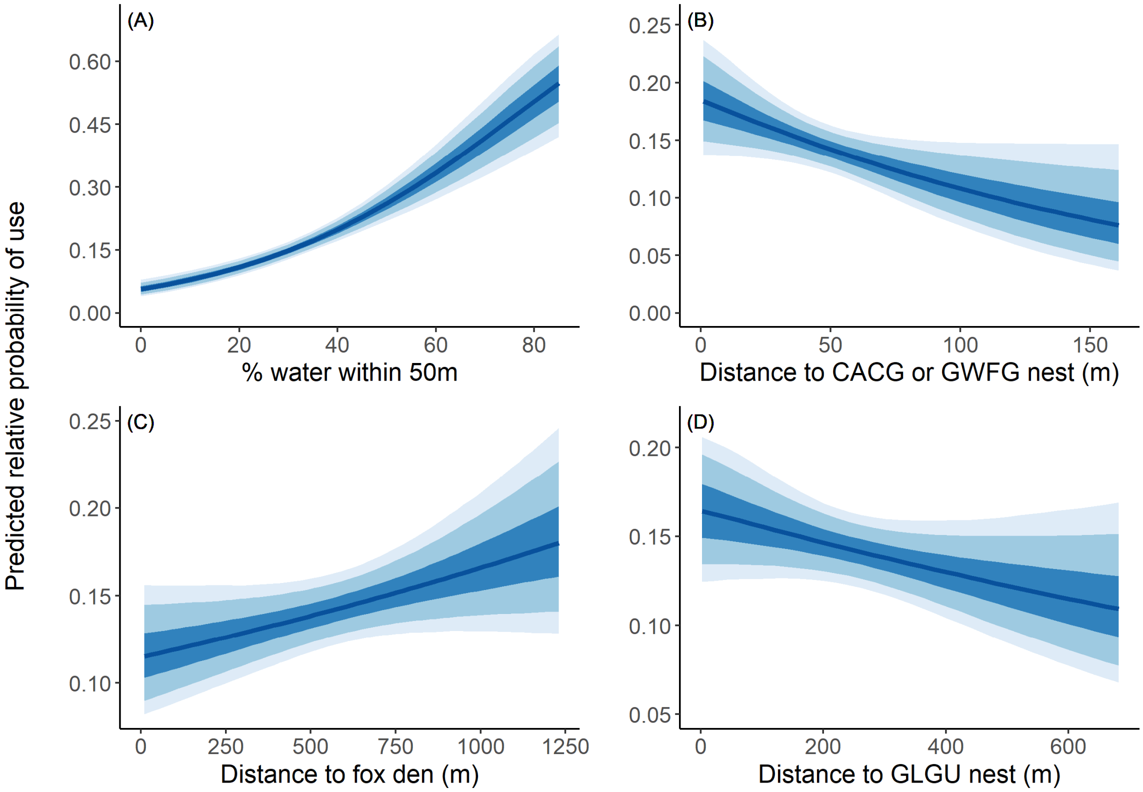

Figure 4-3. Predicted relative probability of use derived from a logistic resource selection model to examine nest-site selection of emperor geese in 2021 on Kigigak Island, Alaska, USA for (A) percent water within 50m of the nest, (B) distance to nearest cackling goose (CACG) or greater-white fronted goose (GWFG) nest, (C) distance to fox den with recent sign, (D) and distance to glaucous gull (GLGU) nest. Envelopes represent 50%, 85%, and 95% credible limits. Predictions were derived with all other variables held constant at their mean.

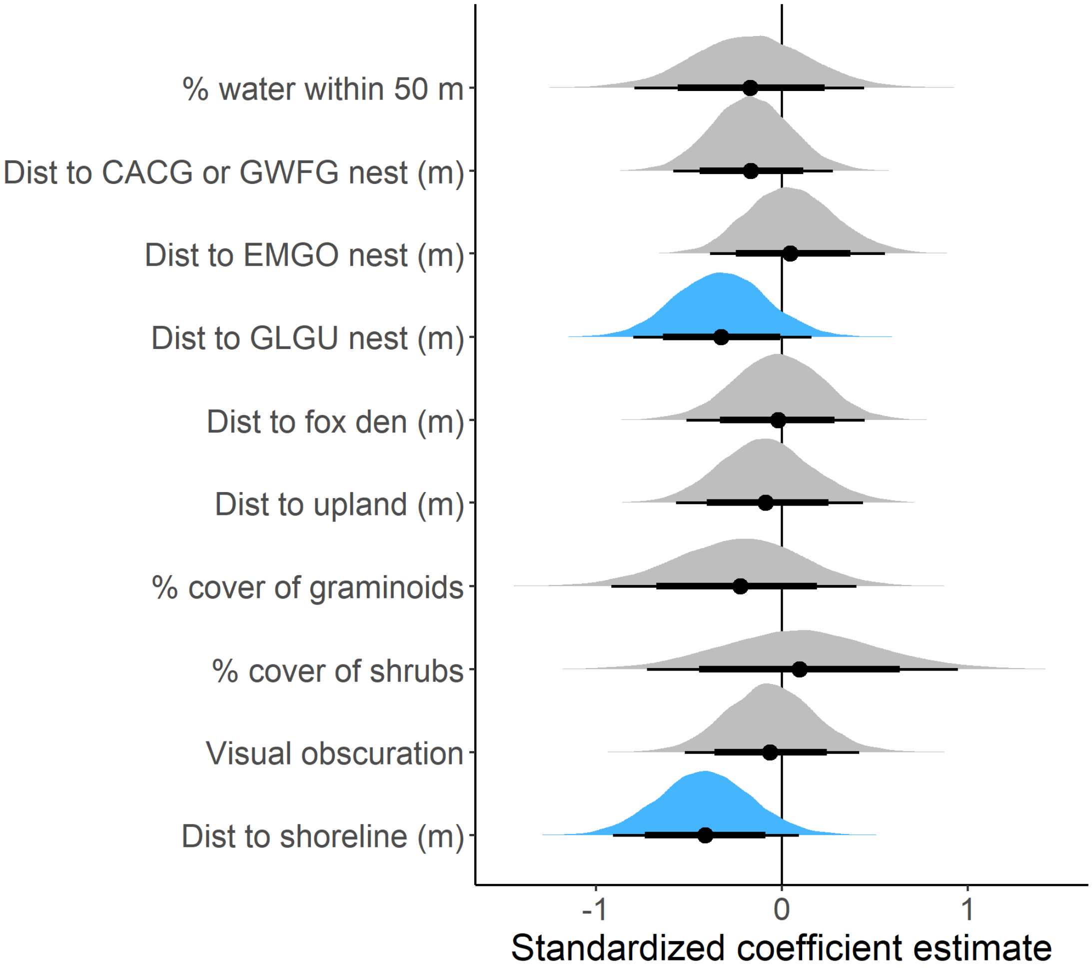

Figure 4-4. Posterior distributions of regression coefficients for the effects of nest-site characteristics on daily survival probability of emperor goose nests monitored in 2021 on Kigigak Island, Alaska, USA. Distributions shaded in blue had strong support for an effect ($f \geq 0.90$), while distributions shaded in grey had weak or no support for an effect ($f < 0.85$). Abbreviations are those used by the U.S. Geological Survey Bird Banding Laboratory.

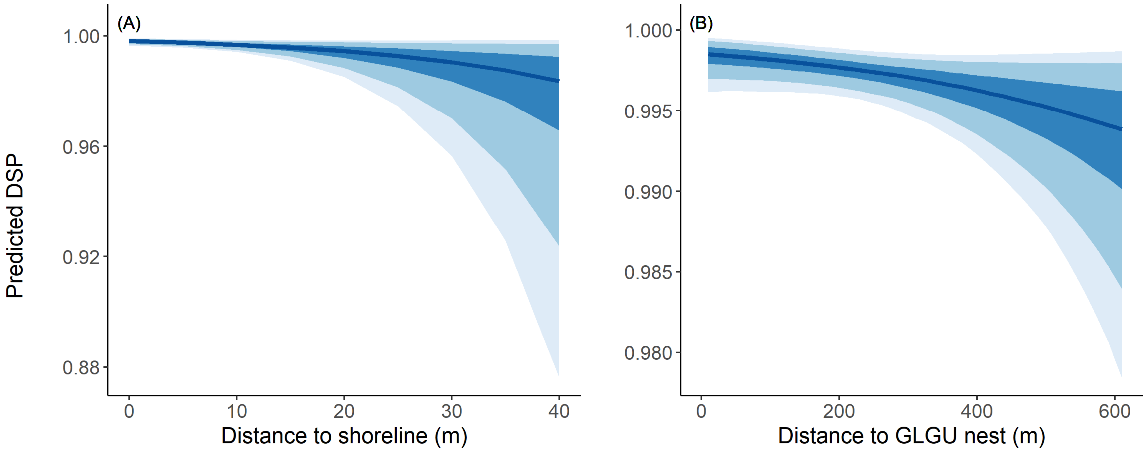

Figure 4-5. Predicted relationship between daily survival probability (DSP) of nests and (A) distance to shoreline and (B) distance to nearest glaucous gull (GLGU) nest from nest survival model for emperor goose nests monitored in 2021 on Kigigak Island, Alaska, USA. Envelopes represent 50%, 85%, and 95% credible limits. Predictions were derived with all other variables held constant at their mean.

TABLES

Table 4-1. Descriptions of predictor variables, expected relationships with nest-site selection and nest survival, and median, minimum, and maximum measurements for nests of emperor geese located in 2021 on Kigigak Island, Alaska, USA and associated random sites.

	Hypothesis		**Median (min–max)**	
Variable	**Selection**	**Nest survival**	**Nest**	**Random**
Distance to nearest emperor goose nest (m)[a]	+	+	63.70 (9.31–257.79)	76.29 (0.97–283.54)
Distance to nearest heterospecific goose nest (m)[a,b]	+	+	39.42 (1.10–112.84)	46.39 (1.02–160.89)
Distance to nearest glaucous gull nest (m)[a]	-	-	191.88 (13.44–609.49)	250.76 (1.87–686.18)
Distance to nearest fox den with recent sign (m)[a]	-	-	640.12 (26.59–1178.33)	564.10 (7.45–1234.46)
Distance to upland (m)[a]	-	-	583.61 (0–1477.65)	554.52 (0–1659.65)
Percent cover of water within 50m[a]	+	+	38.21 (0.42–78.37)	26.61 (0–85.37)
Percent cover of graminoids[c]	+	+	65.00 (13.00–1.00)	77.50 (17.50–100.50)
Percent cover of dwarf shrubs[c]	+	+	0.00 (0.00–77.50)	0.00 (0.00–75.00)
Distance to nearest pond or slough shoreline (m)[c]	+	+	1.05 (0.00–33.49)	3.62 (0.00–41.49)
Visual obscuration[d]	NA	+	0.60 (0.00–1.50)	NA

[a] Variables included in study area scale nest-site selection analysis; includes 225 nests and 1,125 random sites

[b] Includes cackling geese and greater white-fronted geese

[c] Variables included in fine-scale nest-site selection analysis; includes 121 nests and 242 random sites

[d] Included in nest survival analysis only