THESIS

DETERMINING THE IMPACT OF HARVEST AND CLIMATE CHANGE ON THE DEMOGRAPHY OF BLACK BRANT (*BRANTA BERNICLA NIGRICANS*)

Submitted by

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ABSTRACT

DETERMINING THE IMPACT OF HARVEST AND CLIMATE CHANGE ON THE DEMOGRAPHY OF BLACK BRANT (*BRANTA BERNICLA NIGRICANS*)

As a coastal long-distance migrant, black brant (*Branta bernicla nigricans*) are vulnerable to climate and land-use change while also facing harvest pressure from sport hunting along the Pacific Coast. To examine impacts of harvest pressure and environmental change on brant survival and reproductive components of fitness, I combined band-recovery data with live recapture and resighting data from 1990 to 2023 for the Tutakoke River breeding colony of brant on the Yukon-Kuskokwim Delta in western Alaska. I fit multiple Bayesian multistate mark-recapture models to these data to estimate temporal changes in cause-specific mortality and breeding probabilities over the last 33 years. Harvest rate increased over time and is significantly impacted by bag limit across sex and age groups. Adult non-harvest mortality has remained stable over the study period but is higher in years of extreme El Niño and Aleutian Low Beaufort Sea Anticyclone events. Breeding probability for previous breeders increased over time while breeding probability for previous non-breeders decreased, driven largely by differing responses to spring timing. My work describing brant demographic response to environmental change and harvest provides valuable information on how to manage brant most effectively across their migratory range.

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DEDICATION

To my grandfather, David S. Lush, for instilling in me a love for the natural world and mathematics, and for teaching me to approach science and life with wonder.

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Introduction

Migratory species, particularly long-distance migrants, rely on consistent timing and location of resources across broad spatial scales throughout the year, making them vulnerable to changes in their seasonal environments, such as climate change (Foden et al., 2013; Zurell at al., 2018). Long-distance migrants are uniquely affected by changing phenology of food resources and increasingly unpredictable abiotic environmental conditions (Parmesan & Yoh, 2003; Both et al., 2010). This is particularly true for species that breed at high latitudes where climate change has accelerated more rapidly than other parts of the globe, and the ability to anticipate these changes can be challenging because of vast distances between seasonally used habitats (Evans & Bearhop, 2022; Rantanen et al., 2022). These effects may also scale with the life history of species and even individuals, because according to life-history theory (Stearns, 1989), longevity is typically selected for in highly stochastic environments (Metcalf & Koons, 2007; Morris et al. 2008).

Long-lived species with slow life histories (Saether & Bakke, 2000) are typically capable of buffering their chances of survival against unpredictable environmental conditions by, e.g., hedging their bets through diversion of adverse costs onto reduced reproductive effort, such as taking a sabbatical from breeding and waiting for better conditions in the future (Hamel et al., 2010; Culina et al., 2019). But the slow generation turnover associated with longevity may also impede adaptation to trends in mean environmental conditions, such as those affected by long-term climate change. If contemporary environmental change surpasses an organism's ability to cope and survival is affected, it is extremely important to understand underlying causes and consequences of decreased survival in order to effectively manage populations, especially those of long-lived species that are highly sensitive to proportional changes in survival (Pfister, 1998; Heppell et al., 2000; Saether & Bakke, 2000).

Pacific black brant (*Branta bernicla nigricans*; hereafter brant) are a long-lived migratory goose species that could be vulnerable to recent changes in their environments that are occurring across their migratory life cycle. Brant breed in the Arctic and Subarctic and winter as far south as tropical Mexico, whereby most individuals migrate > 35 degrees in latitude twice per year (Ward et al., 2009). But unlike most Arctic geese that have readily shifted away from native wetland plant food during migration and winter to capitalize on agricultural food subsidies concomitant with anthropogenic landscape changes (Abraham et al., 2005; Fox et al., 2017), brant (particularly B. *bernicla nigricans*) have continued to feed exclusively on native coastal wetland plants throughout all seasons (Ward et al., 2005). After leaving the breeding grounds, brant use fragile coastal estuaries (He et al., 2019; Krebs et al., 2023) where they forage on eelgrass (*Zostera sp.*) beds throughout the remainder of their migratory cycle (Reed et al., 1998; Ward et al., 2005). Like other seagrasses, eelgrass beds are sensitive to sea surface temperature (Moore et al., 2012; Hammer et al., 2018) and turbidity (Moore et al., 2012) – both of which are projected to change with ongoing ocean climate change and coastal erosion associated with unsustainable agricultural practices and coastal development (Dowd et al., 2008; Doney et al, 2012; He et al., 2019). Climate processes like the El Niño Southern Oscillation (ENSO) can influence both water temperature and turbidity (via storm frequency). El Niño (as opposed to La Niña) years are associated with higher sea surface temperature and intensified storms over the central Pacific, which may result in poor winter foraging conditions via warmer and more turbid waters (due to storm runoff) along the Pacific coast.

Deteriorated habitat conditions at wintering grounds are of particular consequence to long-distance migrants because competition for food is strong (Lack, 1968), which for capital breeders like brant can often lead to carryover effects on reproduction and other demographic parameters (Harrison et al., 2011). Previous research on brant has documented carryover effects of eelgrass biomass at utilized wintering sites on reproductive phenology, breeding probability, and survival which are amplified by intense ENSO years (Sedinger et al., 2011; Schamber et al. 2012; Riecke, 2020). Though short-term studies of seasonal survival have been conducted on brant (Ward et al., 1997, Ward et al., 2004), there have been few evaluations of how seasonal environmental conditions may affect survival over time.

In addition to environmental conditions at wintering areas, those at the penultimate spring staging grounds along the southern Bering Sea (Ward et al., 2005) may be particularly important during an energetically demanding time after migrating a significant distance, and before major photosynthetic growth of foods, with potential downstream consequences on survival (Reséndiz-Infante & Gauthier, 2024). The Aleutian Low Beaufort Sea Anticyclone (ALBSA) index describes the relative orthogonal position of the Aleutian Low and Beaufort Sea Anticyclone systems in the North Pacific (Stone, 2018). Years of high ALBSA values are indicative of an east-shifted Aleutian Low pressure system (Cox et al., 2017; Stone, 2018) and could be associated with more frequent and stronger storms in the eastern Bering Sea near coastal Alaska (Rodinov et al., 2007). Adverse weather might not only delay brant migration but may also interrupt the ability to forage and at extremes affect thermoregulation, all of which could affect survival of individuals in poor condition. The ALBSA index could thus be another valuable predictor of how environmental conditions near subarctic staging and stopover areas affect brant survival.

At the same time, wildlife harvest, especially of migratory species, can present both an additional risk of mortality and an efficient management tool (Burnham & Anderson, 1984; Cooch et al., 2014). Understanding the joint impact of environmental change and harvest on the survival of migratory species could specifically inform the sustainable management of populations. Sport harvest has partially additive effects on brant mortality, though it is not thought to be the dominant source of mortality (Leach et al., 2017). Accounting for mortality from harvest and other causes allows for more detailed inference about the factors governing mortality dynamics, allowing for managers to decide whether one source of mortality could be managed to mitigate other sources. Previous analysis of brant harvest estimated an increase in harvest-related mortality up until 2015 when the study ended (Sedinger et al., 2022), but managers could benefit from up to date and detailed information about age- and sex-specific harvest rates that could have differential effects on population dynamics.

I developed a Bayesian multistate capture-reencounter model to estimate age-, sex-, and cause-specific mortality associated with sport harvest and other sources. As global change progresses, coastal (Krebs et al., 2023) and (sub)arctic (Rantanen, et al., 2022) habitats that brant rely on are projected to change rapidly, and both El Niño (Cai et al., 2021) and Aleutian Low (Giamalaki et al., 2021) systems are predicted to become more variable and intense. Rapid environmental change may surpass the ability of brant and similar species to buffer survival against increasing environmental variation, or adapt to range shifts in suitable habitat (Wolkovich et al., 2014), which may be additionally impacted by harvest. My objectives are therefore to provide updated information on how harvest and seasonal environmental processes jointly influence the cause-specific mortality components of age- and sex-specific survival, a vital rate that can have substantial impacts on long-term population dynamics (Stahl & Oli, 2006; Koons et al., 2014).

Methods

Study system:

All data collection took place at the Tutakoke breeding colony within the Yukon Delta National Wildlife Refuge in western coastal Alaska. The breeding colony habitat consists of lowland tidal salt marsh at the mouths of the Tutakoke and Kashunuk Rivers dominated by a diverse community of graminoid plants (Sedinger et al 1995; Jorgenson, 2000). The Tutakoke breeding colony is one of several important brant colonies within the Yukon-Kuskokwim Delta of Alaska (Sedinger et al., 1993). While these colonies have undergone a period of long-term decline in abundance (Wilson, 2018), the Tutakoke colony remains an important breeding site for numerous brant.

The majority of brant survival analysis has focused on females (Sedinger et al., 2002; Sedinger et al., 2007; Lindberg et al., 2013; Leach et a., 2017), and there has been no sex-specific analysis of harvest mortality. However, because brant are nearly sexually monomorphic and because highly monogamous breeding pairs migrate together (Nicolai et al., 2012; Leach et al., 2020), I did not expect any difference in male and female harvest or non-harvest mortality since hunter targeting of a specific sex, or sex bias in band reporting, are unlikely and males and females are likely exposed to the same environmental risk throughout the migratory cycle. I did expect that juveniles would be more vulnerable to harvest because juvenile waterfowl are generally more naïve to decoys and thus more vulnerable (Morez et al., 2000; Fowler et al., 2020). I also anticipated that juveniles would have higher and more variable non-harvest mortality over time when compared to fully grown brant, as juveniles in long-lived species are typically less able to buffer survival against environmental variation (Tuljapurkar, 1982).

Data collection:

Mark-recapture data have been collected for brant at the Tutakoke breeding colony since 1986 (Sedinger & Flint, 1995). Brant are captured and given plastic tarsal bands and USGS metal bands at the end of every breeding season just before migration during the remigial molt. The 3-character code and color of individual tarsal bands were read from a distance each breeding season starting when the brant arrived and began nesting, and continued until attempts were made to recapture brant at the end of the breeding season. See Sedinger et al. (1997) for more detailed information about the mark-recapture data collection processes on the breeding grounds.

Information on harvested individuals was obtained from the USGS Bird Banding Lab, after banded birds were shot, retrieved, and bands reported by sport hunters. I included this information on dead individuals to obtain estimates of true survival, as individuals could be harvested anywhere in the brant migratory range, which for the Tutakoke breeding colony, extends from Alaska's Arctic Coastal Plain (Reed et al., 1998) to northwestern Mexico (Reed et al., 1998; Ward et al., 2004; Leach et al., 2019). Due to inconsistent reporting information (Sedinger et al., 2022), I excluded any band returns associated with subsistence harvest by restricting band returns to only those associated with brant shot during the sport harvest season. This may result in slight underestimation of the overall impact of harvest on the brant population, as any subsistence harvest is absorbed into the ‘other’ category of mortality under my model structure (see Analysis).

A refined understanding of how regulations like bag limit and season length affect harvest-related mortality would directly inform the management of brant populations, though there has been little to no previous research on how harvest regulations affect brant harvest rates. In an effort to consider the impact of all brant harvest regulations, I first considered a principal component analysis (PCA) of bag limit and season length set by regional governments across the brant migratory range (Baja Peninsula, California, Oregon, Washington, British Columbia, and Alaska). The PCA resulted in 3 principal components needed to explain the majority of variation in the data but did not significantly reduce the dimensions of brant harvest regulations for interpretation. In most locations, harvest regulations have not changed during the entire study period (1990-2023) and were not highly correlated.

In further effort to identify aspects of harvest regulations that could potentially explain variation in brant harvest rates, I referred to the spatial analysis of brant band recoveries in Leach et al. (2019) to identify the regions where the majority of brant harvest occurred. A large fraction of hunter recoveries of banded brant have come from the Baja Peninsula, Mexico and Humboldt Bay, California (Leach et al., 2019), but bag limit and season length in these locations have remained relatively constant since 1990 (Pacific Flyway Council, 2018; Gary Kramer, pers comm. Steve Olson, pers comm.), and therefore provided no information for explaining changes in annual harvest rates. Information about possible changes in effort among brant hunters in these regions is also lacking (e.g., total days afield each year), in part because the USFWS harvest information program (HIP) captures very few brant hunters in its annual survey of waterfowl hunters (Sedinger et al., 2019). The next highest proportion of brant band recoveries have come from the Izembek Lagoon and Cold Bay region on the Alaska Peninsula, a vital autumn staging area that supports nearly the entire Pacific brant population and where harvest has increased in recent years (Leach et al., 2019). Season length for brant has not changed in Alaska since 1990, but bag limit has varied over time (Pacific Flyway Council, 2018; J. Schamber pers. comm.). In recent years, the number of licensed brant hunting guides has also increased in Cold Bay to accommodate the rising number of out-of-state brant hunters (Jim Sedinger, pers. comm.). This may lead to an increased effect of Alaska bag limit on overall brant harvest rate. I used normalized bag limit in Alaska from 1990-2023 as an index for changes in brant harvest regulations and acknowledge that it could also estimate other factors affecting harvest mortality that are changing in parallel with brant bag limit in Alaska (e.g., changes in migratory phenology that affect where brant are vulnerable to harvest).

In addition to incorporating information on harvest pressure, I also included annual indices for seasonal climatic conditions in my analysis that, as described in the Introduction, may affect forage availability, the ability of brant to forage, migratory phenology, thermoregulation, or a combination of these factors that could scale up to affect morality. While previous research used an annual binary variable to indicate El Niño and non-El Niño years (Sedinger et al., 2006; Sedinger et al., 2011), I used the Multivariate El Niño Southern Oscillation (ENSO) Index Version 2 (NOAA Physical Sciences Laboratory, 2024) and averaged monthly index values from October – March to incorporate more detailed information of (pre-)winter conditions. For reasons described in the Introduction, I expected positive values of the continuous ENSO index to result in deteriorated winter forage and thus higher ‘other’ mortality, and negative values (associated with presumably better forage) to be associated with lower mortality. I also averaged monthly ALBSA index values (Cox et al., 2019) on a continuous scale within each year to obtain an annual index of conditions near staging and breeding grounds.

Analysis:

I used a Bayesian hierarchical analysis of joint live-dead encounters based on a modification of the model originally proposed by Burnham, (1993) to estimate age-, sex-, and cause-specific mortality. To account for differences in mortality and detection between juvenile and adult birds, I developed a multistate version of the mark-recapture model that included three age classes for live detection probabilities: hatch year (HY, the time between near-fledging and approximately age 1), second year (SY, the time between age 1 and 2 when individuals are not yet of breeding age and thus infrequently observed on the breeding grounds), and after second year (ASY, all subsequent ages) birds that are of breeding age (*Fig. 1.1*). I used just two age classes for demographic parameters and dead encounter probabilities based on previous findings: HY individuals were considered juveniles (juv) while SY and ASY individuals were fully grown (*fg*) and constrained to have the same mortality rates and dead encounter probabilities (Leach et al., 2017). The state structure included 7 alive and dead states: alive HY (state 1), alive SY (2), alive and fidel ASY (3), dead juvenile (HY; 4), dead fully grown (SY and ASY; 5), alive and not fidel (6), absorbing dead state (7). I placed the unobservable states 6 and 7 at the end to accommodate MCMC sampling of the multinomial structure of the model (see *Fig. 1.1* and further detail below). My sample included a total of 46,117 released and 2,567 recovered birds across all 34 years of the study (1990-2023), providing a robust sample size. Of the released birds, 22,803 were female and 23,314 were male. Of the released females, 13,217 were released as HY goslings, 637 as SY yearlings, and 8,913 as ASY adults. Of the released males, 12,845 were released as HY goslings, 303 as SY, and 10,166 as ASY. Of the dead recoveries, 1,230 were female (136 recovered as juv and 1091 as fg) and 1,337 were male (136 as juv and 1201 as fg).

Fidelity of ASY brant to natal breeding grounds is known to be relatively high, particularly for females, although dispersal of younger birds regularly occurs (Lindberg et al., 1998; Sedinger et al., 2008). I estimated adult (ASY) and juvenile (HY) fidelity to account for permanently emigrated individuals and attain unbiased estimates of survival. As I did not model any effects specific to individuals, I used an efficient multinomial likelihood parameterization for the multistate model and multinomial-array (m-array) data rather than a state-space likelihood, with separate m-arrays for male and female mark-recapture data. My model was hierarchical in nature consisting of a state-transition matrix ($\Psi_{s,t}$) describing demographic transitions between live and dead states estimated conditionally on a vector of data observation probabilities ($po_{s,t}$). The state-transition matrix $\Psi_{s,t}$ contained age ($juv, fg,$) sex (s), and year (t) specific parameters for survival (S) and fidelity (F):

$$\Psi_{s,t} = \begin{bmatrix} 0 & S_{juv,s,t} * F_{juv,s,t} & 0 & (1 - S_{juv,s,t}) & 0 & S_{juv,s,t} * (1 - F_{juv,s,t}) & 0 \\ 0 & 0 & S_{fg,s,t} * F_{fg,s,t} & 0 & (1 - S_{fg,s,t}) & S_{fg,t,s} * (1 - F_{fg,s,t}) & 0 \\ 0 & 0 & S_{fg,s,t} * F_{fg,s,t} & 0 & (1 - S_{fg,s,t}) & S_{fg,t,s} * (1 - F_{fg,s,t}) & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & (1 - S_{fg,s,t}) & S_{fg,s,t} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

The observation vector $po_{s,t}$ contained age (SY, ASY), sex (s), and year (t)-specific parameters for live detection (p) and a different categorization of age (juv, fg) for dead recovery (r) probabilities:

$$po_{s,t} = \begin{bmatrix} 0 \\ p_{SY,s,t} \\ p_{ASY,s,t} \\ r_{juv,s,t} \\ r_{fg,s,t} \\ 0 \\ 0 \end{bmatrix}$$

Live detection and fidelity (*F*) were both estimated using generalized linear mixed-effects models on the logit scale using *age*- and *sex*-specific intercepts (α) along with annual random effects (ε_t) that were estimated specific to each age and sex in order to attain shrinkage estimates of year-specific parameter values,

$$logit(p_{age,sex,t}) = \alpha_{p_{age,sex}} + \varepsilon_{p_{age,sex,t}}$$

$$logit(F_{age,sex,t}) = \alpha_{F_{age,sex}} + \varepsilon_{F_{age,sex,t}}$$

I used normal priors on the logit scale for intercepts that were vague on the probability scale (Northrup & Gerber, 2018), and normal priors for the annual random effect with vague uniform hyperpriors on variance centered around a mean of zero,

$$\alpha \sim normal(0, 1.5^2)$$

$$\varepsilon_t \sim normal(0, \sigma_t\ )$$

$$\sigma_t \sim uniform(0,2)$$

Detection was fixed to 0 in 2020 when data collection did not occur due to the COVID-19 pandemic.

Recovery of individuals that died from sport hunting was estimated using a derived age, sex, and time-specific Seber r parameter ($r_{age,sex,t}$) (Seber, 1970), which models the probability that a banded bird is recovered and reported conditional on the bird having died. I assumed constant crippling loss (cr) at 0.20 (Bellrose, 1953) and estimated reporting rate (rr) using an informative beta prior – alpha and beta parameters for the beta distribution were moment matched from year-specific 'trophy' reporting rate means and standard deviations provided in Arnold et al., 2020:

$$r_{age,sex,t} = \frac{H_{age,sex,t} * rr_t * (1 - cr)}{1 - S_{age,sex,t}}$$

$$rr_t \sim beta(\alpha_t, \beta_t)$$

where H is the probability of dying from sport hunting (see below and also Cooch et al., 2014).

Mortality probabilities were estimated using linear mixed-effects models on the log-hazard scale for increased interpretability of relative covariate effects (Ergon et al., 2018). The functional relationship between survival probability and the two cause-specific (subscript H: harvest, subscript O: other) mortality hazard rates (haz) can be seen here:

$$S_{age,sex,t} = e^{-(haz_{H,age,sex,t} + haz_{O,age,sex,t})}.$$

The age, sex, and year-specific sport harvest mortality probability is a product of the probability of overall mortality and the hazard ratio,

$$H_{age,sex,t} = \left(1 - S_{age,sex,t}\right) * (\frac{haz_{H,age,sex,t}}{haz_{H,age,sex,t}+haz_{O,age,sex,t}}).$$

The age, sex, and year-specific probability of mortality from other causes is derived via the product of overall mortality and subtraction of the same hazard ratio,

$$O_{age,sex,t} = \left(1 - S_{age,sex,t}\right) * (1 - \frac{haz_{H,age,sex,t}}{haz_{H,age,sex,t}+haz_{O,,age,sex,t}}).$$

It is notable that this parameterization of cause-specific mortality caused any subsistence harvest to be absorbed into the ‘other’ category of mortality. I also note that the derivation assumes sequential causes of mortality (harvest then other sources) throughout the year (Riecke et al., 2022) as opposed to explicit competing risks (Servanty et al. 2010; Koons et al. 2014).

Cause (c)-specific mortality hazards (haz_H, haz_O) were modeled using linear mixed-effects models on the log scale with age and sex-specific fixed effects ($\beta_{cov,age,sex}$) for annual covariates (cov_t) and an annual correlated random effect between sexes ($\varepsilon_{haz_c,age,sex,t}$) to attain annual shrinkage estimates for each parameter constrained by (the potentially highly positive) correlation in mortality between sexes as informed by the data,

$$log\left(haz_{c,age,sex,t}\right) = \alpha_{haz_c,age,sex} + \beta_{cov,age,sex} * cov_t + \varepsilon_{haz_c,age,sex,t}.$$

Normal priors on the log scale were used for cause, age, and sex-specific mortality intercepts that provided vague information on the probability scale,

$$\alpha_{haz_c,age,sex} \sim normal(0, 0.85)$$

as well as for all beta coefficients,

$$\beta_{cov,age,sex} \sim normal(0,10).$$

I used fixed effects for ENSO ($\beta_{ENSO,age,sex}$) and ALBSA ($\beta_{ALBSA,age,sex}$) covariates to explain temporal variation in the ‘other’ category of mortality (which also included any subsistence harvest), and a fixed effect for normalized Alaska bag limit ($\beta_{hp,age,sex}$) to explain temporal variation sport harvest mortality.

When modeling males and females separately during preliminary analysis, I found that male and female mortality posterior distributions broadly overlapped each other for every year of the study (*Supplementary Fig. 1.1*). These preliminary results were consistent across juveniles and adults and led me to directly estimate the apparent close relationship between male and female mortality using an annual correlated random effect on sex-specific mortality hazard rates. I modeled the correlated random effect ($\varepsilon_{haz_c,age,sex,t}$) using a multivariate normal distribution centered around 0,

$$\varepsilon_{haz_c,age,sex,t} \sim MVnormal\left(\begin{matrix}0\\0\end{matrix}, \Sigma_{c,age}\right)$$

with variance-covariance matrices on cause-specific hazards between sexes:

$$\Sigma_{c,age} = \begin{bmatrix} \sigma^2_{c,age,male} & \sigma_{c,age,male} * \sigma_{c,age,female} * \rho_{c,age} \\ \sigma_{c,age,male} * \sigma_{c,age,female} * \rho_{c,age} & \sigma^2_{c,age,female} \end{bmatrix}.$$

Age and sex-specific variance parameters were given vague uniform hyperpriors,

$$\sigma_{c,age,sex} \sim uniform(0, 10)$$

and the age-specific correlation parameters between male and female hazards were given moderately informative uniform priors given preliminary analyses indicated a highly positive relationship,

$$\rho_{c,age} \sim uniform(0, 1).$$

I fit this model in JAGS (Plummer, 2003) with the R (R Core Team, 2022) package jagsUI (Kellner, 2018). I ran the model using 3 MCMC chains for 100000 iterations with a 5000 iteration adaptive period, a burn-in period of 10000 iterations, and a thin rate of 1. I assessed model convergence by calculating $\hat{R}$ for each parameter (Gelman & Rubin, 1992) and by visually inspecting posterior chain mixing.

Results

Parameter variation over time:

The multistate capture-reencounter model achieved convergence with all $\hat{R} < 1.05$ and posterior chains appeared well mixed for all parameters. Across all years of the study, mean annual detection (on the logit scale) of ASY males and females were relatively similar with similar variance (*Table 1.1*), while mean annual detection of SY males was higher than detection of SY females (*Table 1.1, Fig. 1.2*). The annual derived dead recovery probabilities were very similar between adult males (mean = 0.109) and adult females (mean = 0.105) with similar variance (male SD = 0.052, female SD = 0.053), but much lower for juvenile males (mean = 0.020, SD = 0.011) and juvenile females (mean = 0.020, SD = 0.012) (*Fig. 1.3*).

Mean annual adult fidelity was quite high for both males and females while having similarly low annual variance for each sex (*Table 1.1, Fig. 1.4*). Juvenile fidelity was much lower than adult fidelity, and higher and less variable over time for juvenile females compared to juvenile males (*Table 1.1, Fig. 1.4*).

Adult mortality from causes other than sport harvest was considerably lower and less variable over time than for juveniles (*Table 1.1, Fig. 1.5*). Annual correlation between male and female mortality from these causes was estimated close to 1 for both juveniles and adults (*Table 1.2*), confirming my preliminary analysis suggesting similar male and female mortality. The ‘other’ category of mortality across age and sex groups did not exhibit any clear temporal trend but did exhibit signs of cyclic oscillations for juveniles (*Fig. 1.5*).

Sport harvest mortality was similar for all age and sex groups across all years of the study (*Table 1.1, Fig. 1.6*). The estimated annual correlation between female and male sport harvest mortality was close to 1 for juveniles and adults (*Table 1.2*), confirming preliminary results suggesting very similar harvest mortality between males and females. Annual sport harvest mortality increased from 1990 – 2016 across age and sex groups but has not increased further since 2016 (*Fig. 1.6*). Given similarities in cause-specific mortality between sexes, annual survival was also similar between males and females, but lower for juveniles when compared to adults (*Fig. 1.7, Supplementary Table 1.1, Supplementary Table 1.2*).

Covariate effects on mortality:

Mortality from causes other than sport harvest had a weak positive relationship with ALBSA for juvenile females, adult females, and adult males (*Table 1.3*, *Fig. 1.8*). Adult mortality from other causes also had a weak positive relationship with ENSO (*Table 1.3, Fig. 1.8*). While these effects do minimally overlap 0, all Bayesian f-statistics for these effects (proportion of posterior distribution on the same side of 0) were > 0.90, exhibiting clear evidence of relationships (*Table 1.3*). Posterior distributions for ALBSA and ENSO effects on all other age and sex groups broadly overlapped 0 with Bayesian f-statistics < 0.90 (*Table 1.3, Fig. 1.8*).

Sport harvest mortality had a significant positive relationship with Alaska bag limit across all age and sex groups (*Table 1.3, Fig. 1.9*). The effect of bag limit was slightly larger for juveniles than adults and was larger for juvenile females than juvenile males (*Table 1.3, Fig. 1.9*). The effect of bag limit among adults was similar, being slightly larger for adult females when compared to adult males (*Table 1.3, Fig. 1.9*).

Discussion

The demographic buffering hypothesis suggests that in long-lived species, adult survival should be buffered against environmental variation and thus change little in response to environmental stochasticity while juvenile survival is typically lower and varies considerably more over time (Pfister et al., 1998). While my results for temporal variance in survival and mortality was lower for adults compared to juveniles, I found more interannual change in adult survival than expected when considering findings for other long-lived species. Researchers have consistently found or predicted climate change-driven declines in adult survival in other long-distance migrants like white storks (Martín et al., 2021), Kirtland's warblers (Rockwell et al., 2017), and peregrine falcons (Franke et al., 2011) amongst others, which are of consequence on the population dynamics of longer-lived species (Seather & Bakke, 2000). Mortality from causes other than sport harvest for adult brant did not display any clear long-term trends but was more temporally variable than what may be expected for a long-lived species (Saether & Bakke, 2000; Koons et al., 2014). The long-term increase in sport harvest mortality coupled with significant relationships between other sources of mortality (such as natural mortality) and seasonal environmental conditions may require close attention as global change progresses. This is because of the negative influence that variability in vital rates can have on the geometric mean population growth rate (Tuljapurkar, 1990).

I found that fidelity was much higher in adults compared to juveniles and generally higher for females compared to males within each age group - reaffirming previous work on sex and age specific fidelity (Lindberg et al., 1998; Sedinger et al., 2008) and natal dispersal (Lindberg et al., 1998) within this population and in other Arctic geese (Cooch et al., 2001). Juveniles generally experienced lower and more temporally variable fidelity to natal breeding grounds, with juvenile males being less fidel to natal breeding grounds than females, consistent with brant natural history where juvenile males typically disperse to other breeding colonies at a higher rate than females (Lindberg et al., 1998). I found adult brant – particularly females – were extremely fidel to the Tutakoke breeding colony, indicating that once they begin to breed there, they almost never disperse to nest elsewhere – even after taking temporary sabbaticals from breeding (Sedinger et al., 2008).

While fidelity displayed sex-specific disparities, mortality was quite similar between males and females, confirming expectations and previous findings for this population (Leach et al., 2017). Brant are sexually monomorphic (Reed et al., 1998; Leach et al., 2020), largely negating the possibility of hunter targeting or male band reporting bias previously observed in dimorphic harvested waterfowl species (Nichols et al., 1995). Brant also maintain long-term pair bonds with males remaining with female mates throughout the migratory cycle and throughout most of life (Nicolai et al., 2012; Leach et al., 2020). Thus, both males and females experience the same habitat conditions and are exposed to the same degree of environmental variation and harvest risk, resulting in very similar harvest and non-harvest mortality patterns.

Mortality from causes other than sport hunting somewhat followed familiar demographic patterns for long-lived species and did not exhibit any clear long-term trends. Being less able to buffer against environmental variation, juveniles had much higher and more variable mortality from ‘other’ causes over time than adults, consistent with what life history theory predicts for long lived species (Saether & Bakke, 2000). Adult mortality from other causes, however, was more annually variable than expected for a long-lived species, but relationships between these sources of mortality and environmental variables were generally weak or insignificant across most age and sex groups. The lack of a strong response in mortality to broad environmental variation is also consistent with life history theory, as the demographic response to environmental variation for long-lived species is more likely to appear in variation in breeding effort and has been reported in the brant population as a reduction in breeding probability during intense El Niño years (Sedinger et al., 2011) Environmental conditions have been shown to have strong influence on breeding effort (rather than survival) in long-lived income (Culina et al., 2019) and capital breeders (Hamel et al., 2010).

While the effects of environmental variables on mortality were marginal, they were nonetheless present across some age and sex groups and could have a cumulative effect on brant population dynamics in the future. Adult male mortality from other causes was weakly associated with ENSO, while ALBSA had small positive effects on mortality from other causes for both sexes and for juvenile females. Years of high positive ENSO values are associated with warmer, wetter conditions in the central Pacific and potentially degraded winter food resources, while years of high positive ALBSA values are associated with stormier conditions in the North Pacific which could impact brant spring migratory decisions and body condition. Adverse weather along migratory routes have been shown to delay migration departure and arrival (Gordo, 2007) and increase mortality (Newton, 2007; Acker et al., 2021). This consistent positive effect of ALBSA on mortality from other causes across age and sex groups is indicative of the importance of spring climate to mortality dynamics and could signify a protracted increase of seasonal usage of spring staging areas as (sub)arctic winters shorten and springs advance. Preliminary research has also shown a potential trend towards increased brant migratory short-stopping whereby some individuals overwinter at traditional autumn and spring staging areas (Ward et al., 2009). The cumulative effects of increasingly variable conditions in the southern Bering Sea, especially on adult mortality, could have significant impacts on the brant population over time given the high sensitivity of their population growth rate to changes in survival (Pfister, 1998; Cooch et al., 2001; Riecke 2020). Although it should be noted that ENSO and ALBSA are very broad indices of environmental conditions and more data on conditions at staging and wintering areas, and more explicit analysis of long-term change in seasonal mortality dynamics are needed to evaluate the relative demographic importance of these regions and seasons on brant fitness and population dynamics.

The positive associations between seasonal climate variables and mortality from largely natural causes directly emphasize the importance of detailed information of harvest mortality dynamics for effective management. While my results confirmed previous research suggesting a long-term increase in sport harvest mortality of sub-arctic brant through 2015 (Sedinger et al., 2022), I have shown that harvest mortality has not since continued to rise but fluctuated around 0.034 (*Fig. 1.5*) – notably higher than the 33-year mean harvest mortality of 0.021 across age and sex groups. The jump in sport harvest mortality may be due to a change in the Alaska bag limit from 2 to 3 birds a day from 2016-2019, but while the bag limit was lowered back to 2 in 2020, this was not clearly reflected in a lowered harvest mortality post-2020. The persistently elevated harvest mortality could also reflect an increased number of brant hunters (particularly out-of-state hunters in Alaska), but I was unable to model this due to insufficient data on the number of brant hunters in North America over time. The long-term increase in harvest rate was consistent across brant age groups and contrary to my expectations, juvenile birds were no more vulnerable to harvest than adults. Juvenile brant typically stay within family groups throughout their first migratory cycle (Reed et al., 1998) and therefore did not appear to incur any additional harvest risk that can come with being a young inexperienced bird on a hunted landscape (Morez et al., 2000), though their naiveté may enhance the risk of harvest for the entire family.

I indeed found a significant positive effect of bag limit in Alaska on sport harvest mortality across all age and sex groups. Considering the constancy of nearly all other harvest regulations across the brant migratory range, the consistent positive relationship between Alaska harvest pressure and sport harvest mortality may be evidence for harvest as a source of additive mortality in the brant population and not an artifact of stable total harvest and potentially declining abundance (Leach et al., 2017). That said, it is possible that the Alaska harvest pressure covariate may also be capturing inter-annual changes in harvest mortality occurring elsewhere (i.e. Mexico, where the majority of brant are harvested) that may change in parallel with that in Alaska.

Conclusion

Supporting the findings from Leach et al., (2017) who reported long-term declines in juvenile brant survival and more subtle declines in adult survival, I also detected a marginal declining trend in survival (*Fig. 1.6*). But with additional years of data collection, my findings suggest this trend is much more subtle than previously reported, especially for juveniles. And contrary to Leach et al. (2017) who conjectured that declines in survival were in part attributable to range-wide habitat degradation, my cause-specific mortality analyses revealed no evidence of trend in mortality from causes other than sport harvest for adults nor juveniles. My findings do not imply that habitat conditions do not affect mortality, but rather any degradation in habitat might not have been permanent and that habitat may interact with several other factors that collectively cause stochastic fluctuations in natural sources of mortality. More direct analysis of how eelgrass degradation interacts with environmental change and brant demography is needed to understand specific mechanisms behind environmental drivers of brant vital rates. A lack of trend in natural mortality, however, should not induce a state of satisfaction about the future abundance of brant. Further analysis of how seasonal environmental conditions may impact other vital rates like breeding probability via carryover effects, and how breeding decisions may affect mortality, is necessary to get a more complete picture of the environmental drivers of brant demography. Temporal variability in vital rates leads to variability in population growth rates, which in and of itself can reduce long-term population viability (Lande et al., 2003), which is well-known among population ecologist but is sometimes unknown to natural resource managers.

My cause-specific mortality analysis further revealed that subtle long-term declines in survival were more likely the result of increased harvest mortality, which Leach et al. (2017) acknowledged as another possible cause and was previously reported for sub-arctic brant populations but with fewer years of data (Sedinger et al., 2022). The strong significant effect of bag limit across age and sex groups points to the imperative to understand how harvest (and harvest regulations) affects brant mortality and population dynamics, particularly considering the estimated long-term increase in sport harvest mortality coupled with relationships between natural mortality and seasonal environmental conditions that are predicted to become more variable in the future and perhaps even affect long-term availability of seagrass habitat. Informed management of harvest rates could be a powerful and efficient tool to mitigate or compensate for seasonal environmental factors affecting mortality from other causes to maintain a sustainable abundance of brant and a viable sport hunting tradition into the age of increased climate variability (Wolkovich et al., 2014).

Figures & Tables

Table 1.1: Estimated posteriors of overall annual means (α) and inter-annual variances (σ) with corresponding 95% Bayesian credible intervals (CRI) for all directly estimated parameters reported on the link-scale.

Parameter	term	mean (α) (CRI)	variance (σ) (CRI)	link scale
Detection (p)				
	$p_{ASY,m}$	-0.54 (-0.64, -0.39)	0.41 (0.31, 0.53)	logit
	$p_{ASY,f}$	-0.60 (-0.77, -0.42)	0.49 (0.38, 0.64)	logit
	$p_{SY,m}$	-1.14 (-1.48, -0.79)	0.43 (0.01, 1.01)	logit
	$p_{SY,f}$	-2.37 (-2.71, -2.04)	0.65 (0.29, 1.11)	logit
Fidelity (F)				
	$F_{ad,m}$	2.09 (1.90, 2.33)	0.47 (0.25, 0.77)	logit
	$F_{ad,f}$	3.39 (2.99, 3.93)	0.88 (0.43, 1.52)	logit
	$F_{juv,m}$	-2.18 (-2.40, -1.97)	0.15 (0.01, 0.39)	logit
	$F_{juv,f}$	0.02 (-.033, 0.36)	0.54 (0.05, 0.99)	logit
Non-harvest mortality (NH)				
	$haz_{NH,ad,m}$	-1.98 (-2.18, -1.79)	0.47 (0.26, 0.75)	log-hazard
	$haz_{NH,ad,f}$	-2.04 (-2.25, -1.84)	0.53 (0.32, 0.83)	log-hazard
	$haz_{NH,juv,m}$	0.19 (0.04, 0.34)	0.28 (0.18, 0.42)	log-hazard
	$haz_{NH,juv,f}$	0.22 (0.05, 0.38)	0.36 (0.25, 0.51)	log-hazard
Harvest mortality (H)				
	$haz_{H,ad,m}$	-3.73 (-3.88, -3.56)	0.40 (0.29, 0.55)	log-hazard
	$haz_{H,ad,f}$	-3.84 (-4.00, -3.67)	0.44 (0.32, 0.59)	log-hazard
	$haz_{H,juv,m}$	-3.42 (-3.68, -3.15)	0.49 (0.20, 0.85)	log-hazard
	$haz_{H,juv,f}$	-3.41 (-3.68, -3.15)	0.42 (0.13, 0.72)	log-hazard

Table 1.2: Estimated posterior mean, standard deviation (SD), and 95% Bayesian credible intervals (CRI) for the correlation between male and female cause-specific mortality.

Mortality correlation term (ρ)	mean	SD	CRI
$\rho_{NH,juv}$	0.88	0.10	0.61, 1.00
$\rho_{NH,ad}$	0.92	0.09	0.66, 1.00
$\rho_{H,juv}$	0.80	0.19	0.28, 0.99
$\rho_{H,ad}$	0.95	0.05	0.83, 1.00

Table 1.3: Estimated posterior means, 95% Bayesian credible intervals (CRI), and f-values (proportion of posterior on the same side of 0) for fixed-effect coefficients of normalized covariates on non-harvest mortality (ENSO, ALBSA) and harvest mortality (Alaska bag limit). Bolded values denote effects with f-values ≥ 0.90, indicating strong evidence of a relationship.

Covariate	coefficient (β)	mean	CRI	f
ENSO				
	$\boldsymbol{\beta_{ENSO,ad,m}}$	**0.18**	**-0.03, 0.42**	**0.95**
	$\beta_{ENSO,ad,f}$	0.11	-0.11, 0.36	0.83
	$\beta_{ENSO,juv,m}$	-0.02	-0.15, 0.12	0.61
	$\beta_{ENSO,juv,f}$	-0.05	-0.21, 0.10	0.75
ALBSA				
	$\boldsymbol{\beta_{ALBSA,ad,m}}$	**0.15**	**-0.09, 0.39**	**0.90**
	$\boldsymbol{\beta_{ALBSA,ad,f}}$	**0.20**	**-0.04, 0.44**	**0.95**
	$\beta_{ALBSA,juv,m}$	0.06	-0.08, 0.19	0.80
	$\boldsymbol{\beta_{ALBSA,juv,f}}$	**0.10**	**-0.06, 0.26**	**0.90**
Alaska bag limit (hp)				
	$\boldsymbol{\beta_{hp,ad,m}}$	**0.28**	**0.11, 0.46**	**1.00**
	$\boldsymbol{\beta_{hp,ad,f}}$	**0.34**	**0.16, 0.53**	**1.00**
	$\boldsymbol{\beta_{hp,juv,m}}$	**0.38**	**0.11, 0.65**	**1.00**
	$\boldsymbol{\beta_{hp,juv,f}}$	**0.46**	**0.22, 0.71**	**1.00**

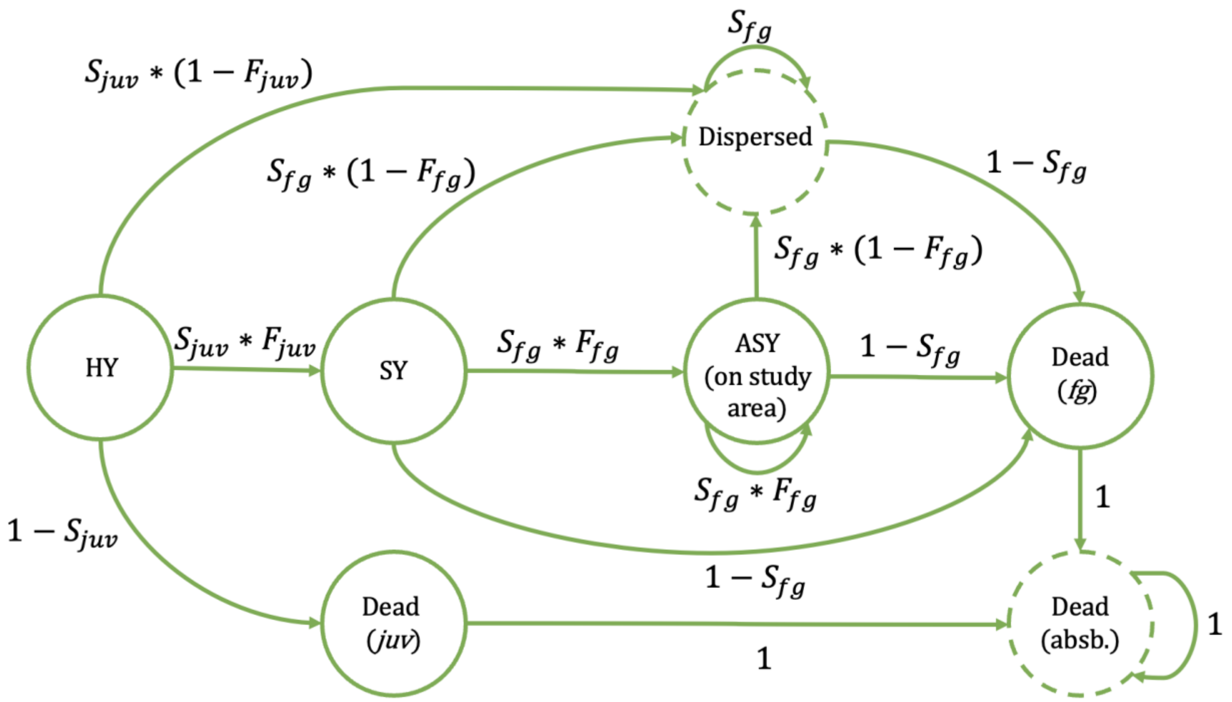

Figure 1.1: Modeled state-transition structure with 7 states: alive HY, alive SY, alive and fidel ASY, dead juvenile (*juv*), dead fully grown (SY and ASY denoted collectively as *fg*), alive and not fidel, and an absorbing dead state. Unobservable states are denoted with dashed circles.

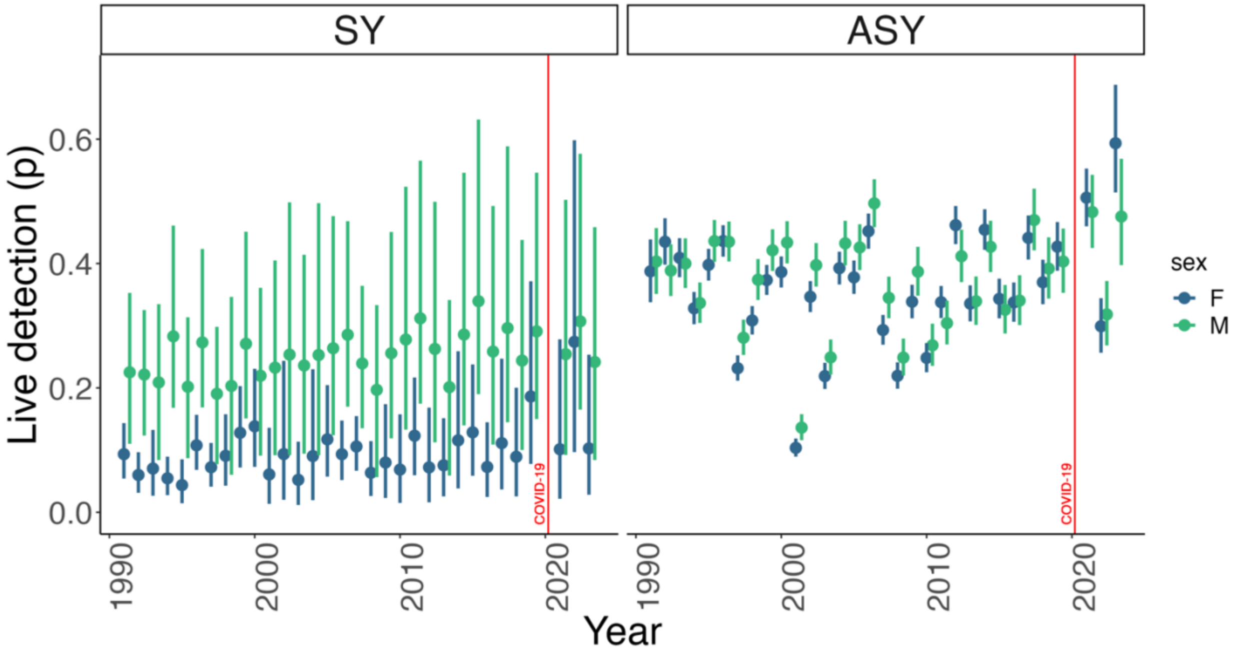

Figure 1.2: Posterior mean annual live detection probabilities (p) of male (green) and female (blue) second year (SY) and after second year (ASY) brant with 95% Bayesian credible intervals. No data collection took place (detection fixed to 0) during the breeding season of 2020 due to the COVID-19 pandemic, marked by vertical red line.

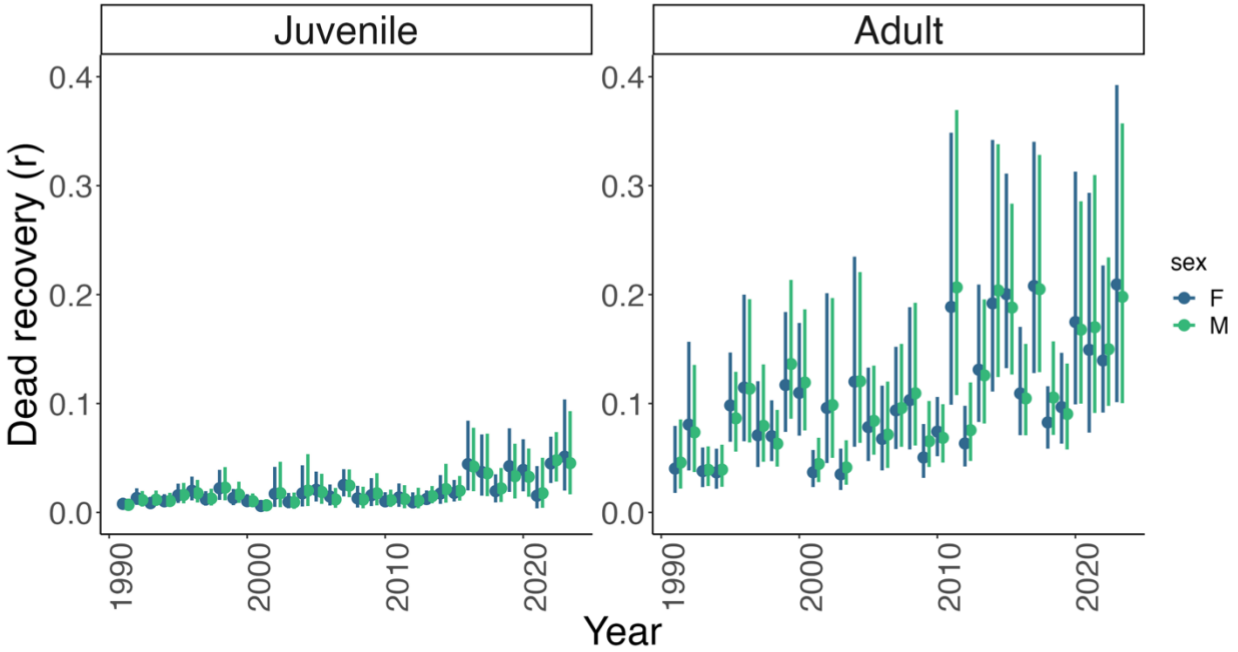

Figure 1.3: Posterior mean annual dead recovery probability (r) of male (green) and female (blue) juvenile and adult brant with 95% Bayesian credible intervals. Dead recovery probability was calculated as the probability a bird is retrieved and reported conditional on the bird being dead.

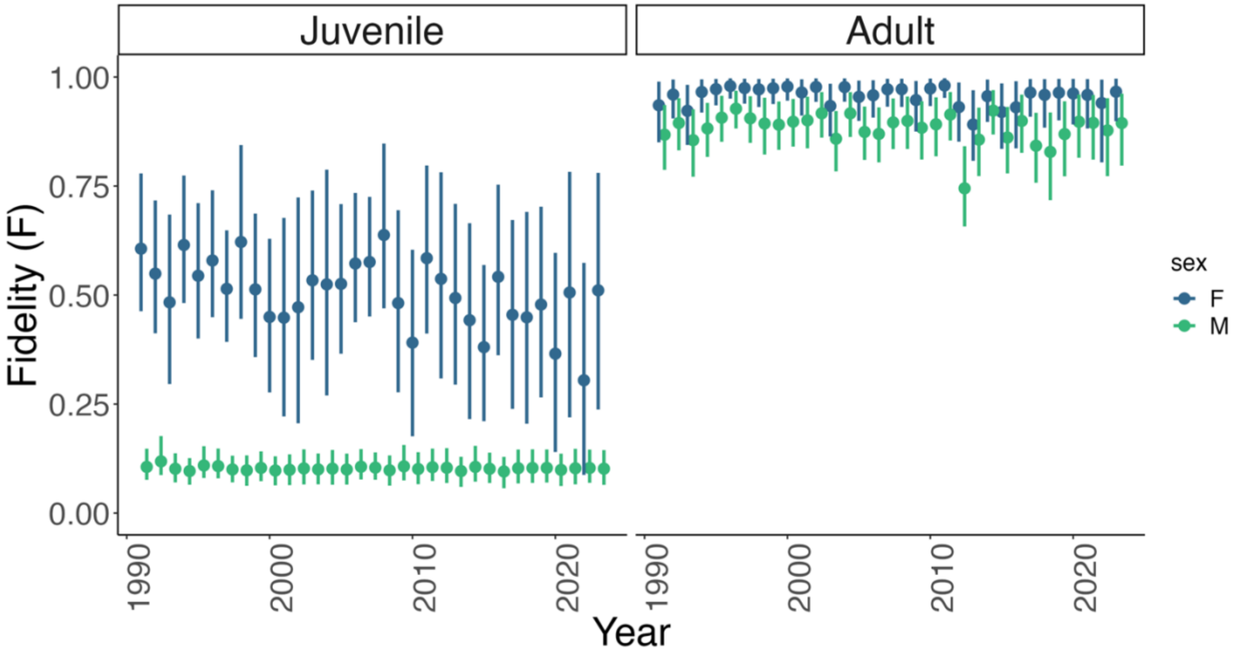

Figure 1.4: Posterior mean annual fidelity probability of male (green) and female (blue) juvenile and adult brant with 95% Bayesian credible intervals. Fidelity probability is the probability of an individual returning to (natal for juveniles) breeding grounds where brant are marked.

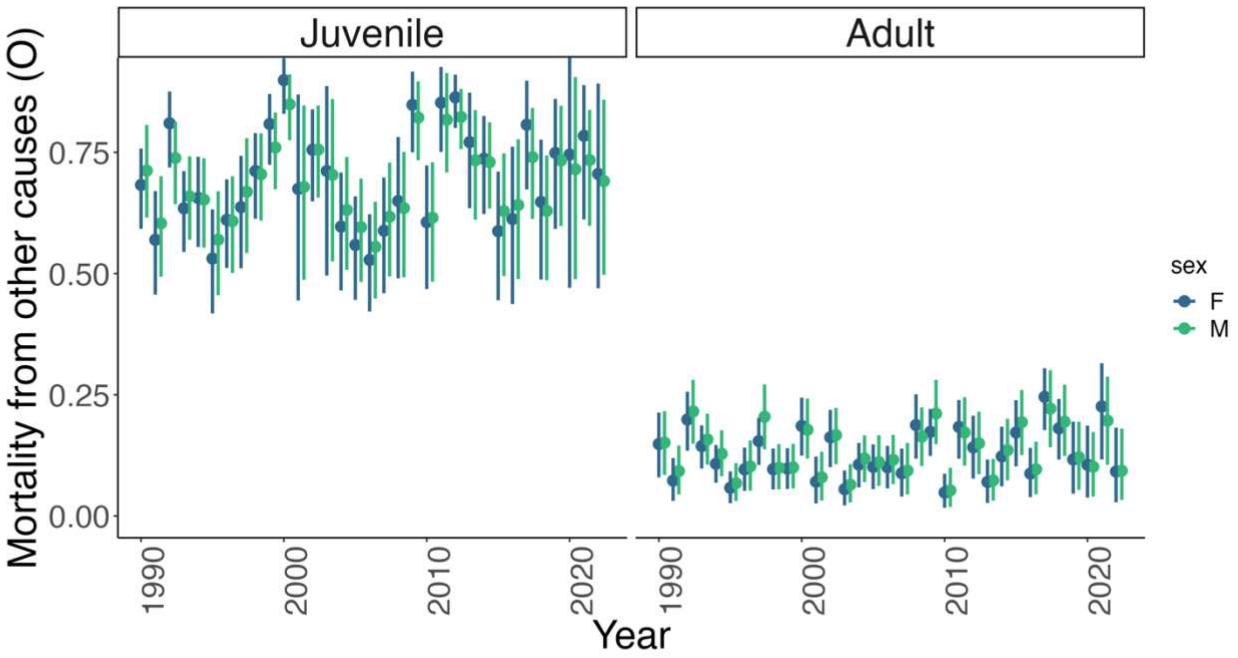

Figure 1.5: Posterior mean annual probability of mortality from causes other than sport hunting for male (green) and female (blue) juvenile and adult brant with 95% Bayesian credible intervals.

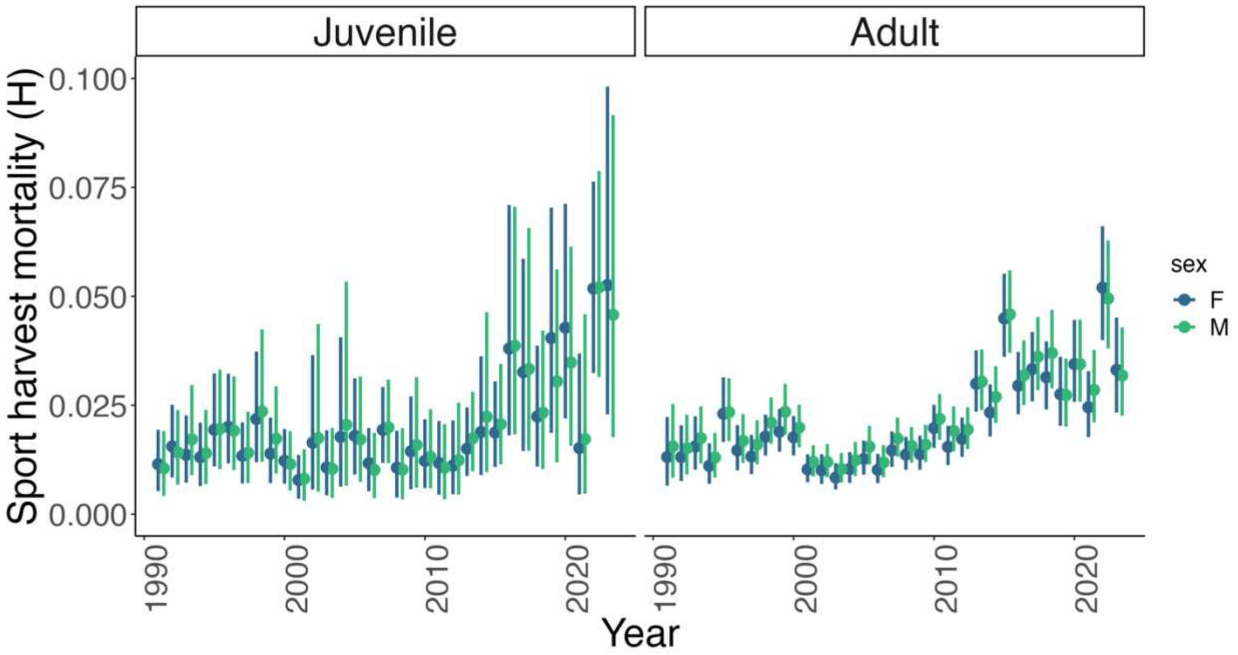

Figure 1.6: Posterior mean annual probability of sport harvest mortality of male (green) and female (blue) juvenile and adult brant with 95% Bayesian credible intervals.

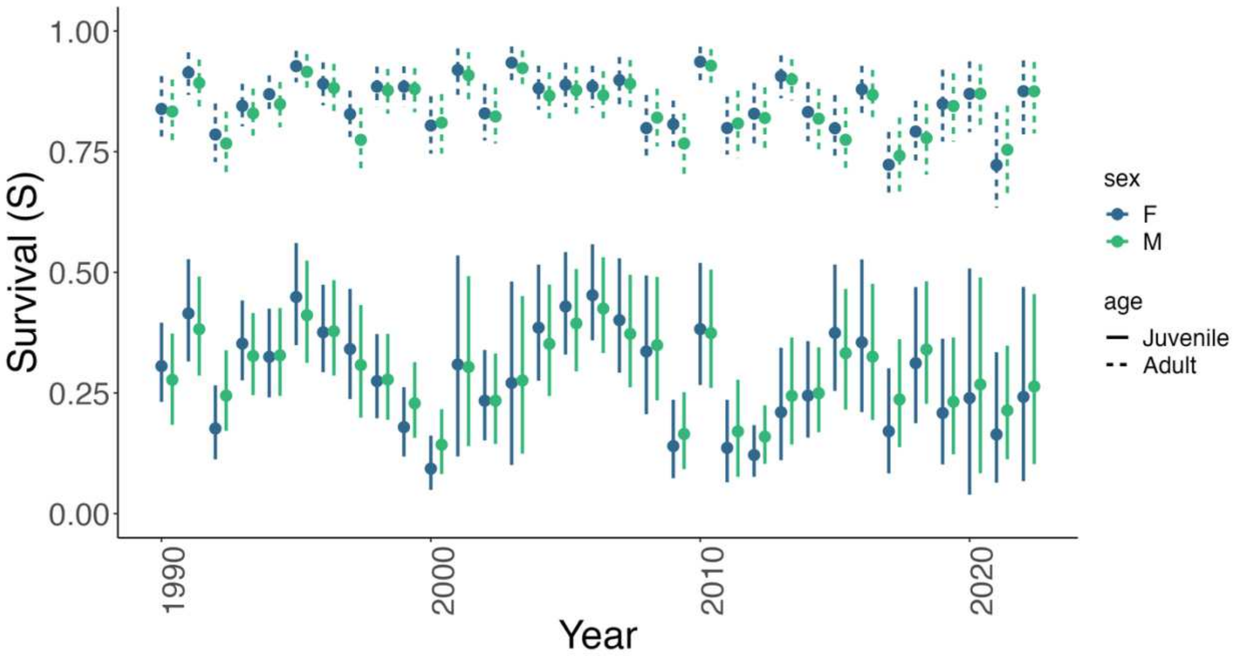

Figure 1.7: Posterior mean annual survival probability of male (green) and female (blue) juvenile (solid) and adult (dashed) brant with 95% Bayesian credible intervals.

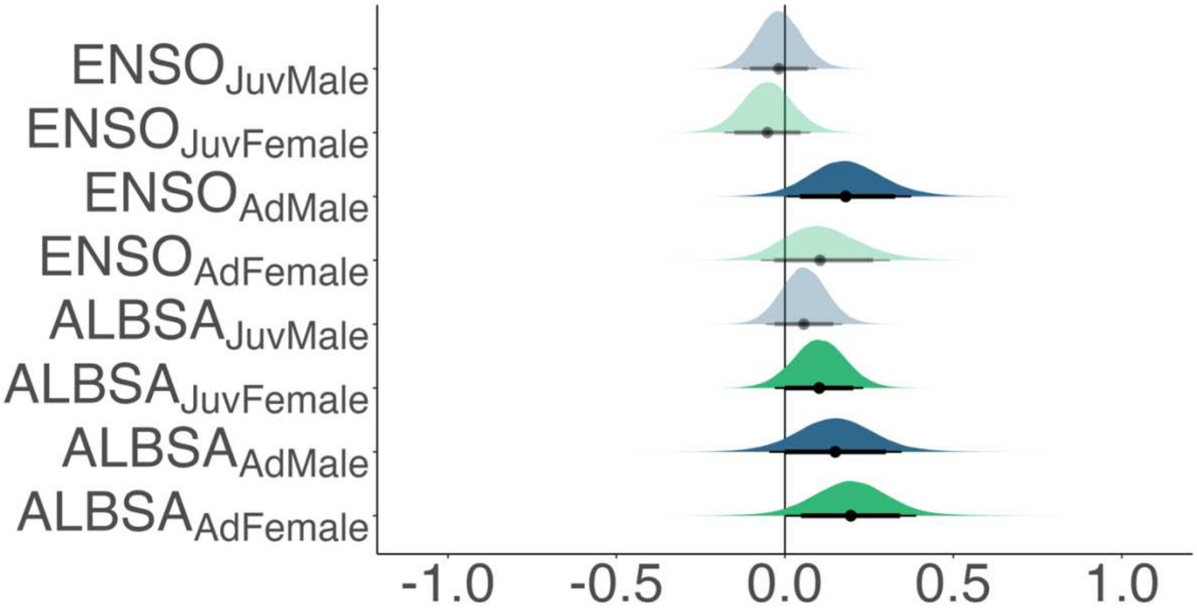

Figure 1.8: Posterior distributions of the fixed-effect β coefficients for normalized sex and age-specific environmental covariates ALBSA and ENSO on the logit scale. Effects on males are shown in green and effects on females are shown in blue. Black dots depict the mean of each posterior and black boxes depict 90% credible intervals. The opacity of the distributions reflect the significance level of the effect - fully opaque distributions have at least 90% of the posterior on one side of 0, while translucent distributions broadly overlap 0.

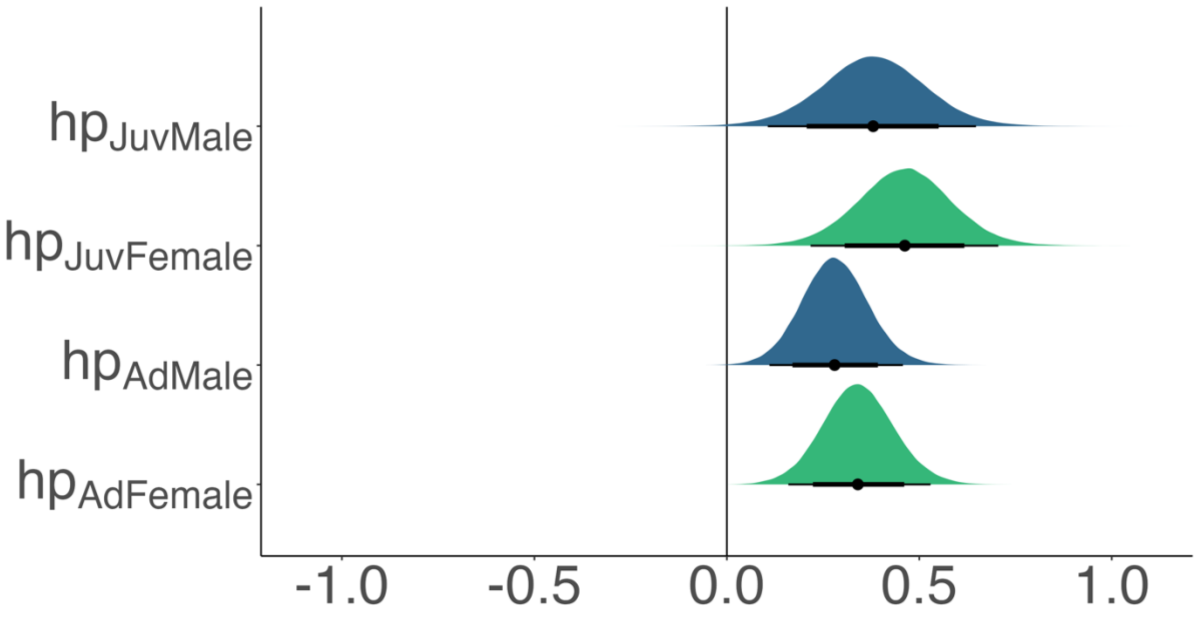

Figure 1.9: Posterior distributions of the fixed-effect β coefficients for a normalized sex and age-specific covariate pertaining to Alaska bag limit (hp) on the logit scale. Effects on males are shown in green and effects on females are shown in blue. Black dots depict the mean of each posterior and black boxes depict 90% credible intervals. The opacity of the distributions reflect the significance level of the effect – all posteriors are fully opaque and have at least 90% of the posterior on one side of 0.

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CHAPTER 2: INVESTIGATING IMPACTS OF ENVIRONMENTAL CHANGE ON MARKOVIAN BREEDING PROBABILITY AND SURVIVAL OF PACIFIC BLACK BRANT

Introduction

Climate change continues to affect wild populations across the globe with varying degrees of severity (Foden et al., 2013). Altered phenology associated with climate change has had particularly consequential effects on long-distance migrants (Zurrel et al., 2018), especially those utilizing arctic and subarctic habitats (Foden et al., 2013) where the effects of climate change have accelerated compared to other parts of the globe (Rantanen et al., 2022). Populations breeding at high latitudes rely heavily on cues and predictable timing of resource availability along their migratory routes (Marra et al., 2005; Winkler et al., 2014), especially near the conclusion of spring migration just before breeding. Many of these species are capital or partially capital breeders that rely on consistent spring phenology and availability of food resources to build the energetic reserves necessary for reproduction (Drent & Daan, 1980; Gauthier et al., 2003; Chudzińska et al., 2016). When spring arrival on the breeding grounds is misaligned with resource availability, a phenological mismatch occurs and is a well-documented consequence of climate change for many long-distance migratory species (Parmesan & Yohe, 2003; Bauer et al., 2008; Both et al., 2010). Advancing springs, particularly near polar latitudes (Høye et al., 2007; Post et al., 2013), have the potential to lead to phenological mismatch for species that historically relied on consistent timing of spring resources, though some species may be better equipped for adapting to increasingly variable seasonal environmental conditions than others.

Species with slow life histories generally cope with environmental stochasticity by buffering highly elastic vital rates (survival) against environmental fluctuations (Metcalf & Koons, 2007; Hilde et al., 2020), but in turn make trade-offs with vital rates (e.g. reproductive investment) that, all else being equal, tend to have less of an effect on fitness (Morris & Doak, 2004). As a result, reproductive investment and reproductive success of long-lived species tend to fluctuate more drastically in stochastic environments, and in turn contribute more to changes in population abundance (Gaillard et al., 2000). The reproductive success of some migratory species has been associated with the ability of individuals to plastically diversify their use of habitats and food to dampen potential effects of a phenological mismatch (Iles et al., 2018). But consistent reductions in breeding probability due to climate-driven habitat degradation, unpredictable environmental conditions, and phenological mismatch could have negative downstream effects on long-term population trajectories. There is mounting evidence that potential declines in abundance of a long-lived migratory goose species, the Pacific black brant (*Branta bernicla nigricans*; hereafter, 'brant') (Wilson, 2018; Sedinger et al., 2019), may be related to climate-driven declines in reproduction (Ward et al., 2018).

Existing individual heterogeneity within populations can result in differential life history strategies for dealing with large scale environmental change (e.g. Jenouvrier et al., 2022). Different migratory strategies have been observed within populations as a response to warmer winters, leading some individuals to delay (Lehikoinen & Jaatinen, 2012; Cox et al., 2023) or short-stop fall migration (Ward et al., 2009; Cox et al., 2023). Degraded seasonal habitat has resulted in differential reproductive strategies within populations, forcing years of skipped breeding in some individuals, which could potentially be related to inabilities of some individuals to consistently acquire the macronutrients needed for reproductive investment (Ward et al., 2005). Differing responses within populations to environmental variation may be a symptom of (or could induce) heterogeneity in fitness, resulting in or exacerbating the difference in fitness between ‘low’ and ‘high quality’ individuals, particularly in long-lived species.

There exists considerable evidence for individual heterogeneity in components of fitness among long-lived species, including fish (Rose & Cowan, 1993; Metcalfe et al., 2015), mammals (Hamel et al., 2009; Chambert et al., 2013; Van de Walle et al., 2020), and birds (Cam et al., 2002; Aubry et al., 2009; Orzack et al., 2011), including brant (Lindberg et al., 2013, Riecke, 2020; Lohman et al., 2021). Heterogeneity within the brant population is not thought to be entirely inherent, but in part a result of habitat conditions on the breeding grounds and a social effect of family size on the wintering grounds (Sedinger et al., 2011; Lohman et al., 2019, 2021), where competition for food resources is most intense (Lack, 1968). Larger family groups tend to despotically secure the best patches of foraging habitat (Reed, 1993; Poisbleau et al., 2006), which could have intensified impact as winter forage habitat deteriorates at broad scales (Ward et al., 2003; Hammer et al., 2018, Krebs et al., 2023), implying that poor competitors suffer from the loss of habitat the most. This phenomenon highlights the direct effect of nest success on procuring quality winter forage, which could lead to higher breeding probability in the subsequent breeding season. Seasonal environmental conditions affecting subsequent seasonal demographic rates, or seasonal carryover effects, have been documented in brant (Ward et al., 2005; Ward et al., 2009; Sedinger et al., 2006) but not in the context of individual heterogeneity.

Environmental processes that influence carryover effects on brant breeding probability could amplify individual heterogeneity within the population. Specifically, broad-scale climate circulations like the El Niño Southern Oscillation have been documented to affect forage on wintering grounds via increased sea surface temperature and storm frequency, effectively diminishing temperature and turbidity-sensitive sea grasses that brant rely on (Ward et al., 2005). Reduced winter forage during intense El Niño years has been shown to result in reduced chances of breeding in the subsequent breeding season (Ward et al., 2005; Sedinger et al., 2006, 2011), but such effects may be especially pronounced for 'lower quality' individuals, or previous failed breeders without family groups on the wintering grounds. In particular, the El Niño Southern Oscillation (ENSO) index can influence both water temperature and turbidity (via storm frequency). El Niño years are associated with higher sea surface temperature and intensified storms over the central Pacific, which may result in poor winter foraging conditions for brant via warmer and more turbid waters (due to storm runoff) along the Pacific coast.

Spring conditions and timing at important spring staging areas and breeding grounds might also influence carryover effects on breeding probability. Stormy spring conditions in the North Pacific could impact the ability of brant to forage and build energy reserves at penultimate spring staging sites on the Alaska Peninsula (Reed et al., 1998; Ward et al., 2009), or even delay arrival at breeding grounds. Later (sub)arctic springs could amount to mismatched nest timing with optimal forage green-up on the breeding grounds (Sedinger & Raveling, 1986; Ross et al., 2017) but could also confer benefits to early arrivals (Prop et al., 2003; Saino et al., 2004) – that have been shown to be 'higher quality' individuals (Lindberg et al., 1997). The Aleutian Low Beaufort Sea Anticyclone (ALBSA) index describes the relative orthogonal position of the Aleutian Low and Beaufort Sea Anticyclone systems in the North Pacific that could efficiently capture aspects of spring weather conditions with ramifications for brant reproduction (Stone, 2018). Years of high ALBSA values are indicative of an east-shifted Aleutian Low pressure system (Cox et al., 2017; Stone, 2018) and could be associated with more frequent and stronger storms in the eastern Bering Sea near coastal Alaska (Rodinov et al., 2007). Adverse weather might not only delay brant migration but may also interrupt the ability to forage, both of which could affect the ability of brant to invest in reproduction, especially for individuals in poor condition.

I examine whether seasonal environmental change (ENSO, ALBSA, and multivariate measure of spring timing) has influenced the dynamics of brant breeding probability, and whether individual heterogeneity helps explain these dynamics. I expect previous non-breeders to subsequently have a lower breeding probability than breeders, as these individuals may be of 'lower quality' and more sensitive to changes in climate regimes influencing seasonal habitat and foraging conditions, thus serially less likely to breed. Sedinger et al. (2008) has shown that previous non-breeders tend to be less likely to return to breed than previous breeders, but did not evaluate the potential mediation of environmental effects on this result. I expect positive extremes of broad-scale climate circulations such as the El Niño Southern Oscillation and Aleutian Low Beaufort Sea Anticyclone to have deleterious effects on breeding probability of both breeders and non-breeders for reasons described above, but more so for previous non-breeders under the 'individual heterogeneity' hypothesis. I expect estimates of spring timing at which nesting habitat becomes available to advance over the course of the study, and to have bolstering effects on breeding probability for both groups, as earlier springs may lead to less expenditure of endogenous resources otherwise spent when waiting for nesting habitat to become available (Hobson et al., 2011; Hupp et al., 2018). Finally, life history theory predicts that in long-lived species, the cost of breeding is unlikely to appear as immediate reductions in survival

(Erikstad et al., 1998), and thus I expected the average adult survival of breeders and non-breeders to be relatively similar.

Methods

Study System:

Mark-recapture data collection took place at the Tutakoke breeding colony within the Yukon Delta National Wildlife Refuge at the mouths of the Tutakoke and Kashunkuk Rivers on the Yukon-Kuskokwim Delta (YKD). The breeding colony is in primarily tidal salt marsh habitat, mainly dominated by graminoid plant species (Sedinger et al 1995; Jorgenson, 2000). See Sedinger et al (1995) for further description of the Tutakoke breeding grounds.

Data Collection:

Capture and marking of brant has occurred at the Tutakoke breeding colony since 1986 (Sedinger et al., 1995). I limited the mark-recapture sample to adult females first released at breeding age (at least 2 years old). I also included individuals first released as goslings or yearlings, who then entered the sample once they were re-encountered on the breeding grounds as breeding-age adults between 1990 and 2023. Brant are captured during brood rearing that coincides with remigial molt for adults, via banding drives in which family groups of brant are herded into pens. All recaptures are recorded, and all unmarked birds are given a metal band identifying them to the USGS Bird Banding Lab in addition to a PVC tarsal band that includes a unique 3-character code and color combination that uniquely identifies the individual for later resighting. Re-encounters occur on the breeding grounds during 3 separate sampling occasions over the course of the breeding season. The first re-encounter occasion occurs when brant first arrive on the breeding grounds and begin nesting. Tarsal bands on marked birds are re-sighted from a distance using spotting scopes, mates assigned, and nests marked and monitored throughout nesting. The second re-encounter occasion occurs during early to middle brood-rearing after a relatively synchronous hatch across the breeding colony. Tarsal bands on marked individuals are then read again using spotting scopes from blinds on 3-7 m tall wooden towers on or near brood-rearing areas. The final re-encounter occasion involves physical recapture during banding drives, roughly a month after hatch. The multiple re-encounter occasion sampling design enables the use of a robust design mark-recapture model (further details provided in Analysis), with the 3 re-encounter occasions serving as secondary sampling occasions and each annual breeding season functioning as primary sampling occasions. Finally, to estimate true (rather than apparent) survival, I incorporated information from harvested marked individuals reported by sport hunters to the USGS Bird Banding Lab as individuals could be harvested from anywhere across the annual migratory range within legal hunting seasons.

To capture relationships between demographic rates and seasonal environmental conditions, I included both direct measures of phenology of spring resources on the breeding and staging grounds as well as broad indices of environmental conditions in my analysis. To describe spring timing on the YKD breeding grounds and at important staging grounds on the Alaska Peninsula, I used a multivariate composite of three variables, which included: the annual date at which snow cover had receded to 10% at the breeding colony (making nesting habitat available), annual median nest initiation date across the breeding colony, and spring (March-May) average sea surface temperature around the Alaska Peninsula staging grounds using data from the NOAA OI SST V2 High Resolution Dataset (Huang et al., 2021). Nest initiation date was used as an index for timing of appropriate hydrological conditions for nesting, as brant cannot nest until snow has melted and excess water has drained off the landscape.

Broad indices of seasonal climatic conditions included the El Niño Southern Oscillation (ENSO) index that is known to influence forage at important wintering grounds along the Baja Peninsula and adjacent areas, and I specifically used the Multivariate ENSO Index Version 2 (NOAA Physical Sciences Laboratory, 2024). To describe conditions near spring staging grounds and during the last leg of spring migration, I used an annual index that describes the orthogonal position of the Aleutian Low and Beaufort Sea Anticyclone (ALBSA) that can be descriptive of temperature and storm frequency in the North Pacific (Rodinov et al., 2007; Cox et al., 2017; Stone, 2018). The predicted effects of these seasonal climate indices on the dynamics of brant breeding probability are described above in the Introduction.

Analysis:

I developed a Bayesian hierarchical version of a multistate capture-reencounter analysis to estimate Markovian breeding and survival probabilities for groups of individuals who either bred or skipped breeding the previous year. The state structure included 3 states: alive and a breeder (state 1), dead (2), and alive and a non-breeder (3) (*Fig. 2.1*). State three was unobservable and placed at the end to accommodate estimation with a multinomial likelihood (explained below). Markovian breeding probabilities were estimated as the probability an individual transitions from either alive state, breeder (B) or non-breeder (NB), to the breeder state in the subsequent year. Survival probabilities were estimated as the probability an individual transitions from either alive state to the dead state or remains in a live state. It should be noted that the state structure does not include a permanently emigrated state, which in turn can have subtle effects on the interpretation of live encounter probabilities. I restricted the sample to only adult females once they had been observed breeding at the study area, after which they will almost never emigrate to another breeding area, allowing me to ignore fidelity in this analysis (but see Chapter 1 adult female fidelity results; Sedinger et al., 2008) and thus focus on other parameters of interest. I included 10,811 adult females that were marked or encountered as adults from 1990-2023 in my sample, 802 of which were recovered dead.

I did not investigate age effects on breeding probability or survival, as attempting to incorporate age effects along with breeding status-specific breeding probability and survival induced issues with parameter identifiability. But because I conditioned my sample on evidence of having bred (the capture methods are heavily targeted at breeders, such as nesting and brood rearing resights, capture of flightless family groups), my results should not be confounded with age effects on recruiting into the breeding population for the first time (i.e., delayed age at first reproduction).

I also did not model individual covariates, which allowed me to use a multinomial likelihood parameterization rather than a state-space likelihood for model efficiency. The model was hierarchical and included a state transition matrix (Ψ_t) with breeding state (B, NB) and year (t)-specific parameters for survival (S) and breeding probability (γ):

$$\Psi_t = \begin{bmatrix} S_{B,t} * \gamma_{B,t} & (1 - S_{B,t}) & S_{B,t} * (1 - \gamma_{B,t}) \\ 0 & 0 & 0 \\ S_{NB,t} * \gamma_{NB,t} & (1 - S_{NB,t}) & S_{NB,t} * (1 - \gamma_{NB,t}) \end{bmatrix}.$$

Demographic transition probabilities were estimated conditionally on a vector of observation probabilities. The observation vector (po_t) includes year (t)-specific parameters for robust design live detection on the primary occasions (p^*) for individuals in the breeding state and a dead recovery parameter (r). Individuals in the non-breeding state are unobservable, so detection for this state was fixed to 0:

$$po_t = \begin{bmatrix} p_t^* \\ r_t \\ 0 \end{bmatrix}.$$

To successfully identify transitions into and out of the unobservable non-breeding state (which is functionally temporary emigration, and cannot be observed), the live detection parameter (p_t^*) was estimated using the full conditional likelihood parameterization of Pollock's robust design (Kendall et al., 1995), following the method detailed in Riecke et al. (2018). The within season re-encounter periods (1:$nest$, 2:$tower$, 3:$band$) were treated as secondary sampling occasions, with the breeding season treated as the primary. Following Riecke et al. (2018), I restructured the three-dimensional individual secondary capture history (individual x primary occasion x secondary occasion) to be summarized as two (primary occasion x secondary occasion) matrices representing the number of individuals encountered conditioned on availability and the total number of individuals conditionally available (observed during at least one secondary occasion) in each secondary occasion. Each secondary occasion detection probability was modeled using these conditional summary matrices with a binomial distribution:

$$N_{110} + N_{101} + N_{111} \sim binomial\big(p_{nest}, (N_{110} + N_{101} + N_{111} + N_{001} + N_{010} + N_{011})\big)$$

$$N_{110} + N_{011} + N_{111} \sim binomial\big(p_{tower}, (N_{110} + N_{011} + N_{111} + N_{100} + N_{101} + N_{001})\big)$$

$$N_{101} + N_{011} + N_{111} \sim binomial\big(p_{band}, (N_{101} + N_{011} + N_{111} + N_{100} + N_{110} + N_{010})\big)$$

where N_{xxx} denotes the number of individuals with a specific type of secondary occasion encounter history for a given primary occasion. To allow secondary (2°) detection probabilities (p_{2°) to vary from year to year, I also included a mean-centered annual random effect on the logit scale for each secondary detection probability,

$$logit(p_{2^\circ,t}) \sim normal(\mu_{p_{2^\circ}}, \sigma_{p2^\circ})$$

with vague hyperpriors on overall mean ($\mu_{p_{2^\circ}}$) and the standard deviation of variance (σ_{p2°),

$$logit(\mu_{p_{2^\circ}}) \sim beta(1,1)$$

$$\sigma_{p2^\circ} \sim uniform(0,2).$$

Data for tower re-encounters (the second secondary sampling period) was not available after 2017, and thus p_{tower} was fixed to 0 from 2018 through the end of the study. No detection information was collected during 2020 due to the COVID-19 pandemic, so all 2° detection probabilities were fixed to 0 in 2020. Finally, primary occasion detection probability (p^*), conditioned on being present, was estimated for each year as a function of the 2° detection probabilities:

$$p_t^* = 1 - ((1 - p_{nest,t}) * (1 - p_{tower,t}) * (1 - p_{band,t})).$$

Annual probabilities of detecting dead individuals reported by hunters was modeled using a time specific Seber *r* parameter (r_t) (Seber, 1970) using a fixed intercept (α_r) and annual random effect (ε_{r_t}) on the logit scale,

$$logit(r_t) = \alpha_r + \varepsilon_{r_t},$$

which estimates the overall probability that among dead birds, the chance the bird was shot, retrieved and reported.

Breeding probabilities ($\gamma_{B,}$, γ_{NB}) were estimated using linear mixed-effect models with fixed effects specific to breeding status ($\beta_{cov_{status}}$) for ENSO, ALBSA, and a structural equation variable for spring timing (ζ_{spring}), plus an annual random effect (ε_t) specific to breeding status.

$$logit(\gamma_{B,t}) = \alpha_{\gamma_B} + \beta_{spring_B} * \zeta_{spring,t} + \beta_{ALBSA_B} * ALBSA_t + \beta_{ENSO_B} * ENSO_t + \varepsilon_{\gamma_B,t}$$

$$logit(\gamma_{NB,t}) = \alpha_{\gamma_{NB}} + \beta_{spring_{NB}} * \zeta_{spring,t} + \beta_{ALBSA_{NB}} * ALBSA_t + \beta_{ENSO_{NB}} * ENSO_t + \varepsilon_{\gamma_{NB},t}.$$

Spring timing ($\zeta_{spring,t}$) was estimated as a latent parameter using a simple structural equation modeling framework (Grace, 2006) cast within a Bayesian capture-recapture framework (Cubaynes et al., 2012) that modeled the combined influence of annual average spring sea surface temperature around the Alaska Peninsula (SST_t), date of 10% snow cover each spring at the breeding colony ($snow_t$), and the median nest initiation date across the brant breeding colony (ID_t). As one might expect, these variables were highly co-linear, and rather than pick only one to best represent spring timing near breeding and spring staging areas, using this structure to model the interaction between these terms as a latent covariate ($\zeta_{spring,t}$) representing spring timing allowed me to incorporate information among all three components of spring timing. Observed values of each measured variable were normally distributed with the mean modeled as a linear function of latent spring timing,

$$SST_t \sim normal\left(\alpha_{SST} + \beta_{SST} * \zeta_{spring,t}, \sigma_{SST}\right)$$

$$snow_t \sim normal(\alpha_{snow} + \beta_{snow} * \zeta_{spring,t}, \sigma_{snow})$$

$$ID_t \sim normal(\alpha_{ID} + \beta_{ID} * \zeta_{spring,t}, \sigma_{ID}),$$

where the left-hand side of each random variable above are data. I used a structure for the latent spring timing random term ($\zeta_{spring,t}$) that can help with MCMC chain mixing and thus model convergence, in which $\zeta_{spring,t}$ is derived from a standard normal variable ($\zeta^{*}_{spring,t}$) multiplied by a gamma distributed variance term ($\sigma_{\zeta_{spring}}$),

$$\zeta_{spring,t} = \zeta^{*}_{spring,t} * \sigma_{\zeta_{spring}}$$

$$\zeta^{*}_{spring,t} \sim normal(0,1)$$

$$\sigma_{\zeta_{spring}} \sim gamma(1,1).$$

All explanatory variables were normalized, and all variable-specific intercepts (α_{var}) were given mildly informative normal priors based on measured values. All beta coefficients (β_{var}) were given vague normal priors, with one fixed to 1 to aid in identifiability and to fix the scale of the latent spring timing parameter ($\zeta_{spring,t}$) to that of nest initiation date (β_{ID}) (Cubaynes et al., 2012),

$$\alpha_{var} \sim normal(0,1)$$

$$\beta_{SST} \sim normal\ (0,10)$$
$$\beta_{snow} \sim normal\ (0,10)$$
$$\beta_{ID} = 1,$$

and vague gamma priors were used for all variance terms,

$$\sigma_{var} \sim gamma(1,1).$$

While the multistate structure described above (*Fig. 2.1*) allows for both breeding probability and survival to differ between previous breeders and non-breeders, parsing breeder from non-breeder survival proved difficult because non-breeders were unobservable, and I had no additional information to inform survival of individuals in this state. To aid in identifiability of the model, I used posterior distributions of annual adult male brant survival from the same study area and time period (i.e., results from Chapter 1 for adult male survival) with moderately inflated variance as an informative beta prior for non-breeder survival. Annual mean and (inflated) variance of adult male survival ($S_{ad,m}$) were moment matched to alpha ($\alpha_{S_{ad,m}}$) and beta ($\beta_{S_{ad,m}}$) shape parameters for the beta distribution used to model non-breeder survival,

$$S_{NB} \sim beta(\alpha_{S_{ad,m}}, \beta_{S_{ad,m}}).$$

Non-breeding females would have similar energetic demands as a breeding male, and previous research has also shown adult brant male and female survival to be very similar (Chapter 1 adult survival results), thus adult male survival was used as an informative prior of female non-breeder survival. Survival of breeders was estimated using a simple linear mixed-effect model on the logit scale with a fixed intercept (α_{S_B}) and an annual random effect ($\varepsilon_{S_B,t}$),

$$logit(S_{B,t}) = \alpha_{S_B} + \varepsilon_{S_B,t}.$$

For all intercepts (α), I used normal priors on the logit scale that were vague on the probability scale (Northrup & Gerber, 2018),

$$\alpha \sim normal(0, 1.5^2).$$

All annual random effects (ε_t) were modeled using a parameterization identical to that used when modeling ζ_{spring} above that aided in MCMC chain mixing (T. Riecke, pers. comm.), in which ε_t is derived by multiplying a standard normal variable (ε_t^*) with a gamma distributed variance term (σ_t),

$$\varepsilon_t = \varepsilon_t^* * \sigma_t$$

$$\varepsilon_t^* \sim normal(0,1\ )$$

$$\sigma_t \sim gamma(1,1).$$

The multistate mark-recapture model was developed in a Bayesian framework and fit using JAGS (Plummer, 2003) run from the R software using the jagsUI package (Kellner, 2018). I ran the model for 200000 iterations, discarded the first 50000 iterations as burn-in and saved every 10th iteration. Model convergence was assessed by calculating $\hat{R}$ for all monitored parameters (Gelman & Rubin, 1992) and by visually examining chain mixing.

Results

The multistate capture-reencounter model achieved convergence, with $\hat{R} < 1.05$ for all parameters and visually good mixing among chains. Across all years of the study, secondary detection probability during nesting (p_{nest}) was highest, followed by detection during banding (p_{band}), and then detection during tower resighting (p_{tower}) (*Fig. 2.2, Table 2.1*). Robust design primary detection (p^{*}), as functionally expected, was higher than any secondary detection probability for all years of the study (*Fig. 2.2*). Recovery probability (r) was estimated to be generally lower than all other live detection probabilities except p_{tower}, and remained relatively stable over time (*Table 2.1*).

Survival probability was very similar between previous breeders and non-breeders, with respective credible intervals overlapping for every year of the study (*Fig. 2.3, Table 2.2*). Survival, while having broader credible intervals of precision, was approximately three orders of magnitude less annually variable than breeding probability for each group (*Table 2.2*).

Breeding probability of previous breeders was consistently higher than breeding probability of previous non-breeders (*Fig. 2.4, Table 2.2*), and both breeding probabilities varied considerably from year to year (*Fig. 2.4, Table 2.2*). Simple loess (local regression) curves fit to the estimated annual breeding probability posteriors revealed a long-term decline in the probability of previous non-breeders returning to breed in subsequent years (*Fig. 2.4*), while breeding probability of previous breeders appeared to increase over time *(Fig. 2.4)*.

The ENSO index did not have any clear effect on breeding probability of either group, while ALBSA had a strong negative relationship with breeding probability of previous non-breeders but no relationship with previous breeders (*Fig. 2.5, Table 2.3*). Spring timing had significant ($f > 0.90$, f being the proportion of the coefficient posterior on the same side of zero as the median) and opposite effects on breeding probability for previous breeders and non-breeders (*Fig. 2.5, Table 2.3*).

Discussion

While Markovian breeding probability (and other types of temporary emigration) can be difficult to estimate in migratory species (Kendall & Pollock, 1992; Kendall et al., 1995), it can provide detailed insight into the dynamics of individual breeding effort within a population (e.g., Kendall & Nichols, 1997; Bailey et al., 2004; Converse et al., 2009). My use of a multistate robust design (MSRD) model structure allowed me to parse non-breeding from non-detection within this population and estimate for the first time the effects of long-term seasonal environmental conditions on brant investment into breeding. This analysis also implicitly allowed for differential survival between breeding and non-breeding individuals, which previous MSRD maximum likelihood analyses of breeding probability for brant could not achieve (Sedinger et al., 2008, 2011; Nicolai & Sedinger, 2012).

Though constraining survival of non-breeders to an informative prior based on male survival partially limits our ability to make any strong inference about the cost of breeding within this population, it also made biological sense given the similar energetic demands of a male and non-breeding female, and given previous findings (Ch. 1) indicating strong similarity in brant survival between sexes for all age groups. Model constraints implicitly allowed for differences in survival between breeders and non-breeders, but the data and model indicated that they were quite similar, confirming expectations and previous findings for other long-lived species (Bohec et al., 2007; Weimerskirch, 1992). Life history theory predicts that in long-lived species, the immediate cost of breeding typically appears in future breeding effort rather than survival (Stearns, 1992), but long-term studies of individually-marked animals are increasingly revealing the delayed costs on earlier onset or more rapid rates of actuarial or reproductive senescence late in life (e.g., Reed et al., 2008; Aubry et al., 2009, 2011; Boonekamp et al., 2014). Individual heterogeneity within populations is nevertheless known to mask evolutionary tradeoffs (survival vs breeding; van Noordwijk & de Jong, 1986; Metcalf, 2016) for which there is mounting evidence in brant (Lindberg et al., 2013; Riecke, 2020; Lohman et al., 2021). Our findings suggest heterogeneity within this population, but do not rule out the possibility of a simultaneous cost of breeding on future reproductive performance, later in life (i.e. senescence), and may require model parameterizations that account for more detailed aspects of individual heterogeneity (e.g., individual mixture distributions alongside Markovian dynamics) (Pledger & Schwarz, 2002; Lindberg et al., 2013).

Breeding probability of previous breeders was consistently higher than non-breeders (e.g. Sedinger et al. 2008, 2011) and provided further support for the individual heterogeneity hypothesis within the brant population. Other mark-recapture studies of long-lived populations have found similar evidence of heterogeneity in Markovian breeding dynamics (Cam et al., 2002; Bohec et al., 2007; Chambert et al., 2013; Desprez et al., 2017). For brant, these results likely represent a combined effect of nest success (and clutch size) on breeding probability through the social dominance of family groups on critical foraging grounds, and inherent heterogeneity in individual fitness within the population that influences reproductive success, the ability to acquire resources, or both. Future work could decouple the direct influence of brood size at hatch (a surrogate for family size migrating to non-breeding areas and conferred foraging opportunity) from other inherent qualities of individual heterogeneity by experimentally manipulating brood size at hatch and assessing carryover effect on fitness components, such as breeding probability.

Evidence for heterogeneity in brant is abundant, but my results showing long-term divergence in Markovian heterogeneity of individual breeding dynamics (*Fig. 2.3*) suggest differing responses to environmental change within this population that could further amplify inequalities among individual breeding investments. The ALBSA index had a significant negative effect on breeding probability for previous non-breeders but not for breeders (*Fig. 2.4, Table 2.2*), partially explaining the different temporal dynamics for these groups of individuals. The negative effect of ALBSA refers to lowered breeding probability in years of highly positive ALBSA values, which can be associated with increased storm frequency near coastal Alaska (Cox et al., 2019) and presumably worsened conditions on staging grounds on the Alaska Peninsula. Previous non-breeders are likely not part of a family group and may be in worse condition than previous breeders, having been relegated to subpar forage at winter or migratory staging grounds due to lower social status (Poisbleau et al., 2006; Sedinger et al., 2011), thus less able to cope with adverse weather and subsequently more likely to skip breeding.

Spring timing had opposing effects on breeding probability for breeders and non-breeders (*Fig. 2.4, Table 2.2*), exacerbating apparent differences in fitness between the two groups (*Fig. 2.3*) as spring timing advanced over time (*Supplementary Fig 2.1, Supplementary Fig 2.2*) and with spring phenology projected to keep advancing (Høye et al., 2007; Post et al., 2013; Xia et al., 2015). Earlier springs were associated with lower breeding probability for previous non-breeders, but higher breeding probabilities for previous breeders, partially driving the long-term opposing trends in heterogeneous breeding probability as spring timing was estimated to have advanced (i.e. trending toward earlier dates) over the course of the study (*Supplementary Fig. 2.1*).

Sedinger et al. (2011) found higher breeding probability for individuals utilizing higher-quality forage areas at wintering grounds on the Baja Peninsula, while Ward et al. (2009) showed increased numbers of brant wintering on the Alaska Peninsula presumably because of warmer and shorter winters. My results may suggest differential fitness of diverging migration strategies between previous breeders and non-breeders. Earlier spring timing could confer benefits to previous breeders because of their superior ability to acquire resources that could fuel earlier and more rapid spring migration back to the breeding grounds (Daunt et al., 2014), potentially allowing them to 'match' advancing springs and reap fitness benefits (Both et al., 2005). Yet, annual climate warming associated with earlier springs may also be leading to an increased proportion of non-breeding brant wintering on the Alaska Peninsula. Though this saves the energy required to migrate long distances, it might also come at the cost of subsisting on meager forage during seasons when photosynthesis cannot occur, which could result in poor body condition that requires a greater length of time to replenish in the spring and potentially necessitating skipped breeding to replenish the reserves necessary to survive. Such processes may be exacerbated in years with high positive ALBSA values consistent with my findings.

Unlike previous analyses (Ward et al., 2005, Sedinger et al., 2006, 2011), I did not detect an effect of ENSO on breeding probability. This may be due in part to my use of a continuous measurement of ENSO (MEIv2) rather than a binary variable representing El Niño versus non-El Niño years (Sedinger et al., 2006, 2011); my longer time series of data; or perhaps because I considered other explanatory variables along with ENSO. The lack of an effect of ENSO could also be due to an increased proportion of individuals wintering in Alaska rather than along the Baja Peninsula, but this is unlikely as the majority of YKD brant are still wintering in Mexico (Leach et al., 2019).

The increasing trend over time in breeding probability of previous breeders could in part be explained by an age effect on breeding probability itself, e.g., if the consistently successful breeders become older and more experienced (Aubry et al., 2009; Pradel et al., 2012; Chambert et al., 2013), breeding probability of previous breeders may increase (Sedinger et al, 2008; Nicolai & Sedinger, 2012).

Conclusion

I did not examine environmental effects on survival, but inter-annual variation in survival was estimated to be roughly 3-fold smaller on the logit scale than that of breeding probability for either group (*Table 2.2*), suggesting that the response to environmental variation in this population occurs as variation in breeding investment, and less so through adult survival. If heterogeneity between breeders and non-breeders in this population is exacerbated by future environmental change and relegates an increasing portion of the population to non-breeder status, there could be drastic consequences on population viability. These insights into environmentally sensitive vital rates like breeding probability are difficult to obtain without long-term marking and monitoring programs. Current and future effects of environmental change on highly responsive vital rates like breeding probability should be considered in both study design and conservation of critical seasonal habitat for long-lived migratory species.

Figures & Tables

Table 2.1: Posterior estimates for the inter-annual means and standard deviations of temporal variance on the logit scale for detection parameters, with associated 95% Bayesian credible intervals.

Detection parameter	term	mean (α) (CRI)	Variance (σ) (CRI)
Secondary detection (p)	p_{nest}	-0.05 (-0.22, 0.13)	0.47 (0.35, 0.62)
	p_{tower}	-3.47 (-4.16, -2.79)	1.75 (1.38, 1.99)
	p_{band}	-1.23 (-1.54, -0.94)	0.84 (0.62, 1.14)
Dead recovery (r)	r	-2.50 (-2.71, -2.28)	0.58 (0.42, 0.78)

Table 2.2: Posterior estimates for the inter-annual means and standard deviations of temporal variance for directly estimated demographic parameters on the logit scale, with associated 95% Bayesian credible intervals.

Demographic parameter	term	mean (α) (CRI)	variance (σ) (CRI)
Survival probability (S)	S_B	1.68 (1.54, 1.83)	0.28 (0.15, 0.44)
Breeding probability (γ)	γ_B	1.006707 (0.69, 1.34)	1.11 (0.60, 1.62)
	γ_{NB}	-1.333239 (-1.62, -1.07)	1.01 (0.32, 1.49)

Table 2.3: Posterior means of coefficients for explanatory variables, 95% Bayesian credible intervals, and *f*-values for normalized covariate effects on breeding probability (γ) for previous breeders (B) and non-breeders (NB) on the logit scale. Bolded coefficients represent effects for which *f* ≥ 0.90, indicating evidence of a relationship.

Covariate	coefficient (β)	mean	CRI	*f*
ENSO	$\beta_{ENSO,B}$	-0.05	(-0.35, 0.25)	0.64
	$\beta_{ENSO,NB}$	0.01	(-0.23, 0.26)	0.52
ALBSA	$\beta_{ALBSA,B}$	-0.06	(-0.37, 0.26)	0.64
	$\boldsymbol{\beta}_{\boldsymbol{ALBSA,NB}}$	**-0.30**	**(-0.58, -0.04)**	**0.99**
Spring timing	$\boldsymbol{\beta}_{\boldsymbol{spring,B}}$	**-0.57**	**(-1.31, -0.10)**	**0.99**
	$\boldsymbol{\beta}_{\boldsymbol{spring,NB}}$	**0.27**	**(-0.09, 0.73)**	**0.93**

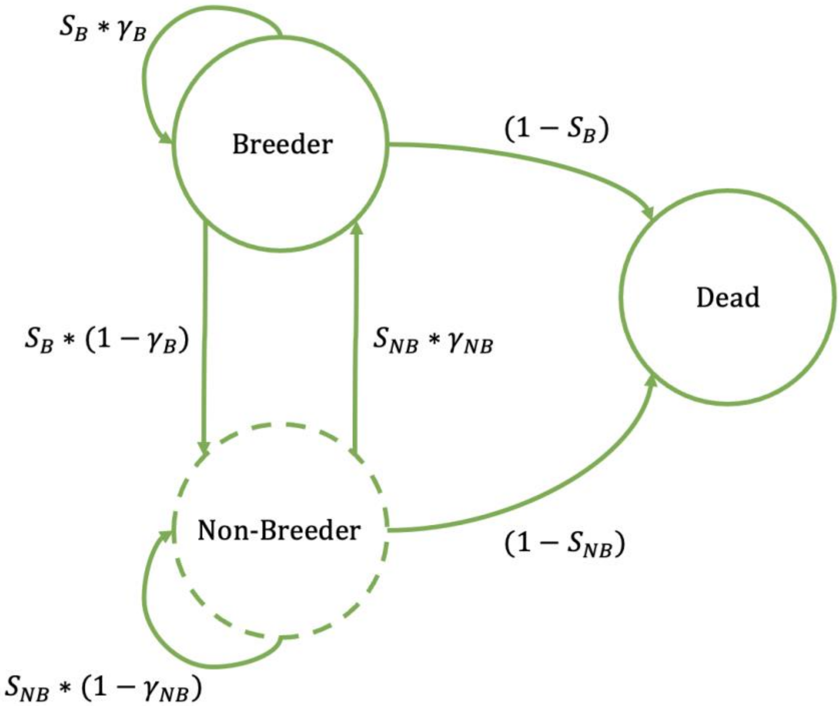

Figure 2.1: State transition structure with 3 states: alive and on the breeding grounds (Breeder), dead, and alive and not on the breeding grounds (Non-Breeder). The non-breeder state is hidden, or unobservable (denoted by dashed circle).

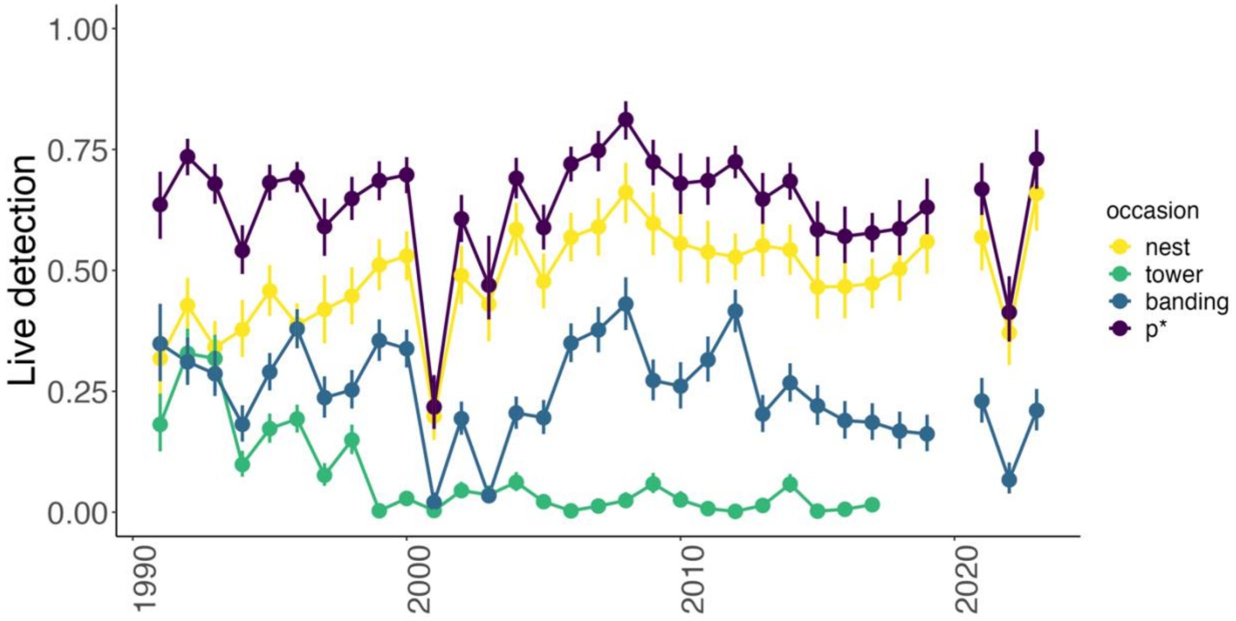

Figure 2.2: Estimated posterior means (dots) for annual live detection probabilities, with secondary detection probabilities for the nesting period (1: yellow), the tower resight period (2: green), and the banding period (3: blue). Primary detection probabilities (p^*) are shown in purple. Error bars represent 95% Bayesian credible intervals.

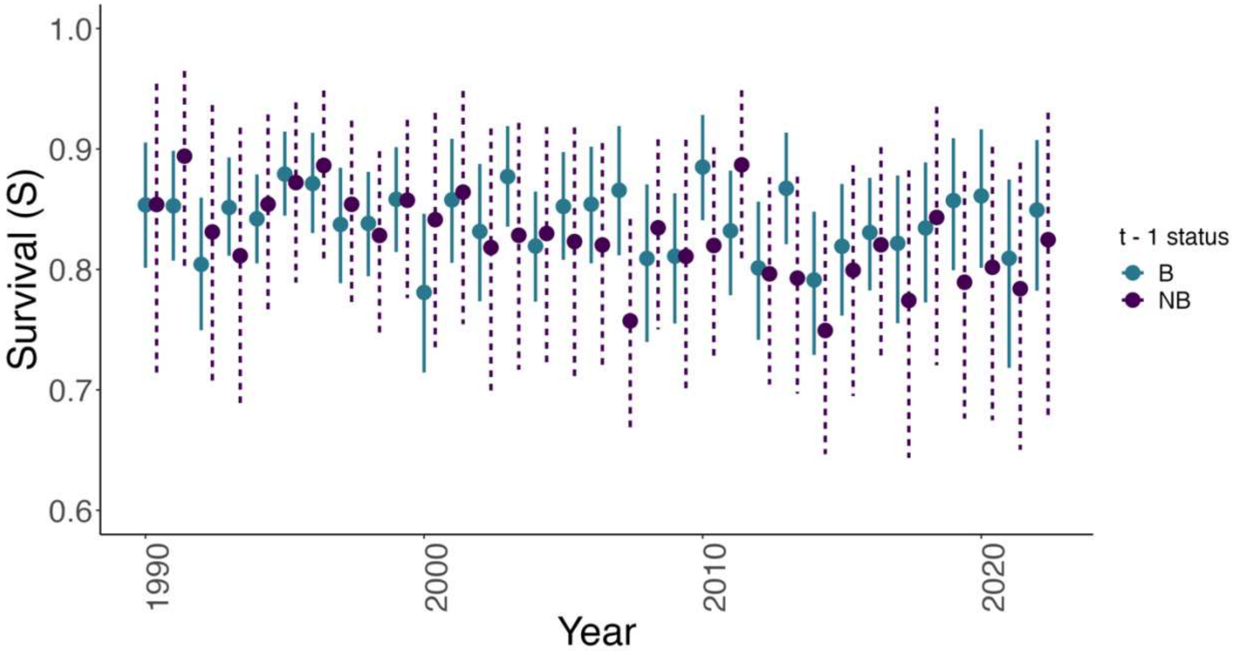

Figure 2.3: Estimated posterior means of annual survival probabilities (S) for previous breeders (B: blue, solid) and non-breeders (NB: purple, dashed). Error bars denote 95% Bayesian credible intervals.

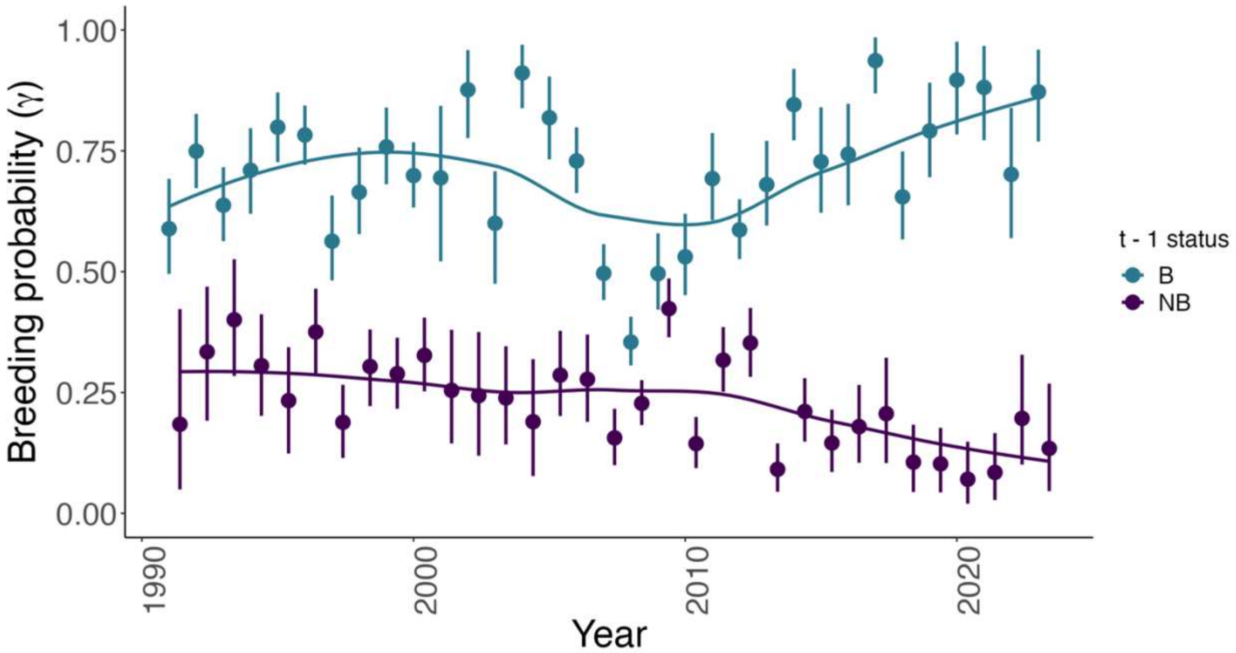

Figure 2.4: Estimated posterior means of annual breeding probability (γ) for previous breeders (blue) and previous non-breeders (NB) at time *t*-1, with corresponding loess curves fit post hoc to the estimates to illustrate trends over time. Error bars represent 95% Bayesian credible intervals.

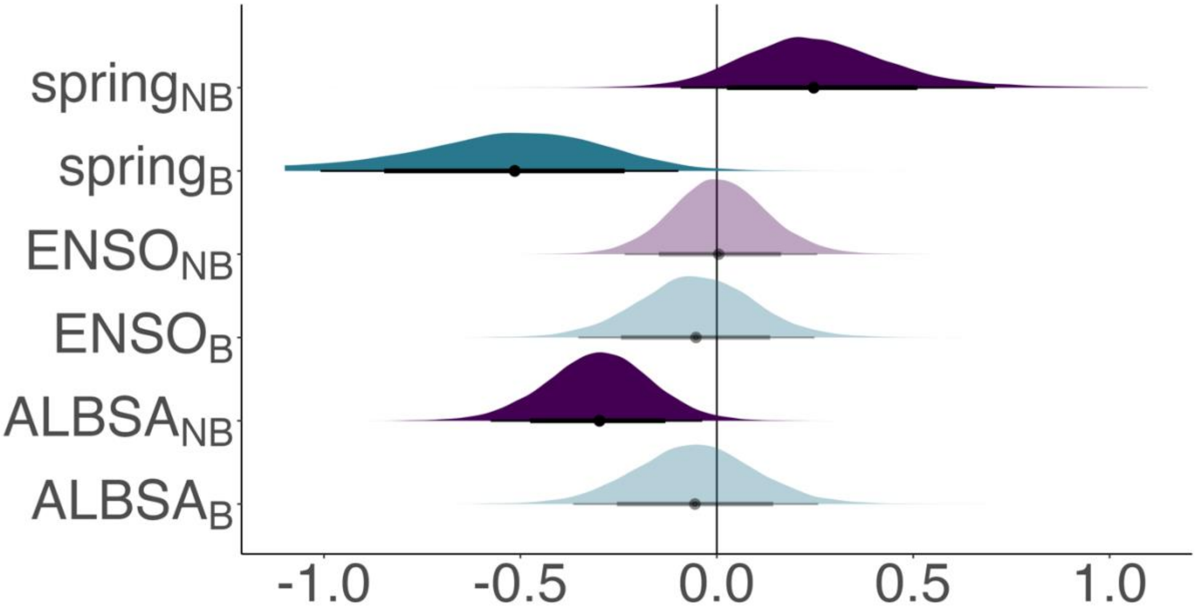

Figure 2.5. Estimated posterior distributions of normalized coefficients (β) of environmental covariates on breeding probabilities of previous breeders (B: blue) and non-breeders (NB: purple). Opacity of the distributions represents the significance of the effect, with opaque distributions having *f*-values ≥ 0.90, or greater than 90% of the distribution on the same side of zero as the median, showing evidence of a relationship. Translucent distributions broadly overlap zero, and do not indicate evidence of a relationship. Black lines under each distribution represent 95% quantiles, while black boxes represent 80% quantiles.

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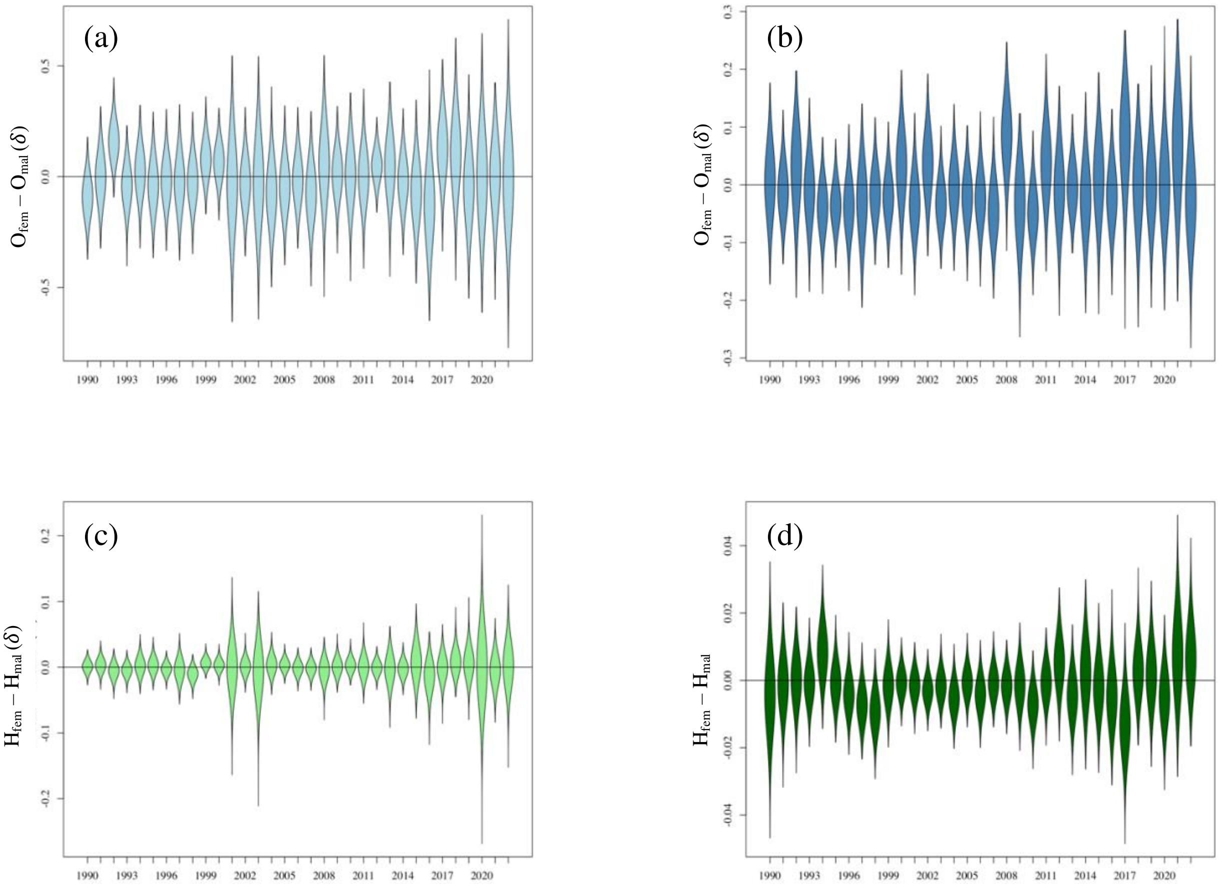
APPENDIX

Chapter 1 Supplementary Materials



Supplementary Figure 1.1: Differences (δ) between female and male annual estimated posterior distributions of mortality from other causes (O) for juveniles (panel a) and adults (panel b) and of sport harvest mortality (H) for juveniles (panel c) and adults (panel d).

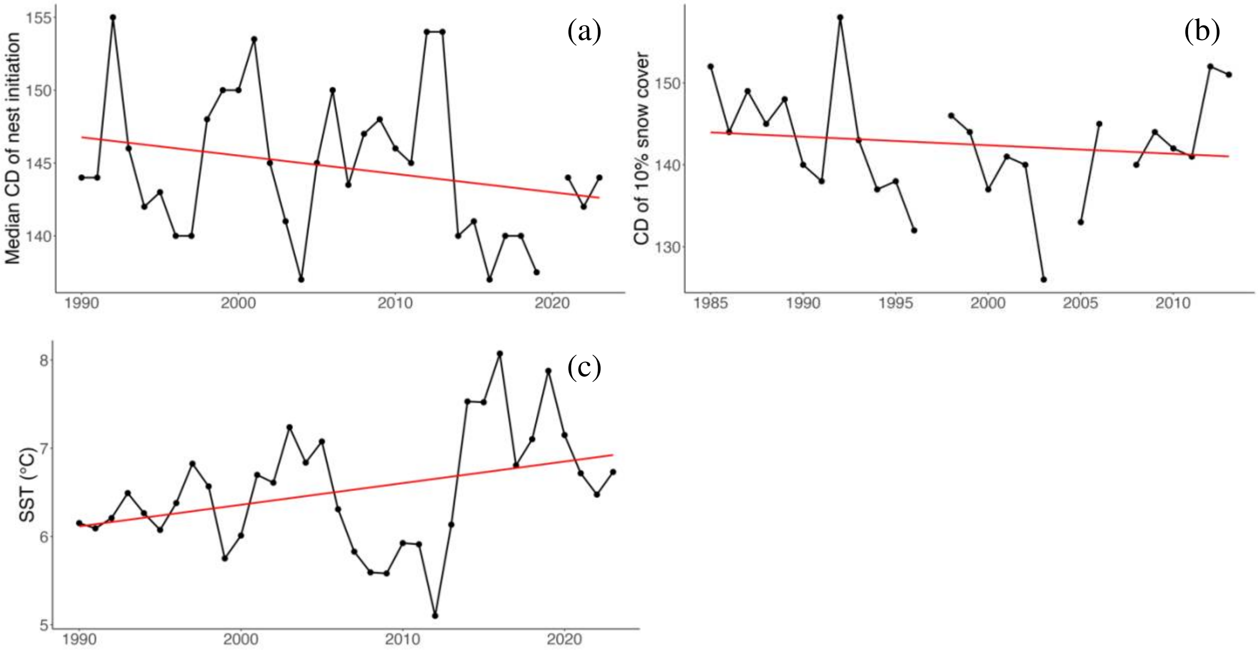
Supplementary Table 1.1: Estimated posterior mean annual survival probability with associated 95% Bayesian CRI in parentheses for each age and sex group.

Year	$S_{ad,m}$	$S_{ad,f}$	$S_{juv,m}$	$S_{juv,f}$
1990	0.83 (0.77, 0.9)	0.84 (0.77, 0.91)	0.28 (0.18, 0.37)	0.31 (0.23, 0.40)
1991	0.89 (0.84, 0.94)	0.91 (0.87, 0.96)	0.38 (0.29, 0.49)	0.41 (0.32, 0.53)
1992	0.77 (0.70, 0.83)	0.79 (0.73, 0.85)	0.24 (0.17, 0.34)	0.18 (0.11, 0.27)
1993	0.83 (0.78, 0.88)	0.84 (0.80, 0.89)	0.33 (0.25, 0.42)	0.35 (0.28, 0.44)
1994	0.85 (0.80, 0.89)	0.87 (0.83, 0.91)	0.33 (0.24, 0.43)	0.32 (0.24, 0.42)
1995	0.92 (0.87, 0.95)	0.93 (0.89, 0.96)	0.41 (0.31, 0.52)	0.45 (0.35, 0.56)
1996	0.88 (0.83, 0.93)	0.89 (0.85, 0.93)	0.38 (0.29, 0.48)	0.38 (0.29, 0.47)
1997	0.77 (0.71, 0.84)	0.83 (0.78, 0.88)	0.31 (0.20, 0.43)	0.34 (0.24, 0.47)
1998	0.88 (0.83, 0.92)	0.88 (0.84, 0.93)	0.28 (0.19, 0.37)	0.27 (0.20, 0.37)
1999	0.88 (0.83, 0.92)	0.88 (0.84, 0.93)	0.23 (0.16, 0.31)	0.18 (0.12, 0.26)
2000	0.81 (0.75, 0.87)	0.80 (0.75, 0.87)	0.14 (0.08, 0.22)	0.09 (0.05, 0.16)
2001	0.91 (0.86, 0.96)	0.92 (0.87, 0.96)	0.30 (0.14, 0.49)	0.31 (0.12, 0.54)
2002	0.82 (0.77, 0.88)	0.83 (0.77, 0.89)	0.23 (0.14, 0.33)	0.23 (0.15, 0.34)
2003	0.92 (0.88, 0.96)	0.93 (0.90, 0.97)	0.28 (0.12, 0.45)	0.27 (0.10, 0.48)
2004	0.87 (0.82, 0.91)	0.88 (0.84, 0.93)	0.35 (0.24, 0.47)	0.39 (0.28, 0.52)
2005	0.88 (0.82, 0.93)	0.89 (0.84, 0.93)	0.39 (0.29, 0.51)	0.43 (0.33, 0.54)
2006	0.87 (0.82, 0.92)	0.88 (0.84, 0.93)	0.42 (0.33, 0.53)	0.45 (0.36, 0.56)
2007	0.89 (0.83, 0.94)	0.90 (0.85, 0.95)	0.37 (0.26, 0.50)	0.40 (0.29, 0.53)
2008	0.82 (0.76, 0.88)	0.80 (0.74, 0.87)	0.35 (0.23, 0.49)	0.34 (0.21, 0.49)
2009	0.77 (0.70, 0.83)	0.81 (0.76, 0.86)	0.17 (0.09, 0.25)	0.14 (0.07, 0.24)
2010	0.93 (0.88, 0.96)	0.94 (0.90, 0.97)	0.37 (0.26, 0.51)	0.38 (0.27, 0.52)
2011	0.81 (0.74, 0.88)	0.80 (0.74, 0.86)	0.17 (0.08, 0.28)	0.14 (0.06, 0.24)
2012	0.82 (0.75, 0.88)	0.83 (0.76, 0.89)	0.16 (0.10, 0.22)	0.12 (0.08, 0.18)
2013	0.90 (0.86, 0.94)	0.91 (0.86, 0.95)	0.24 (0.14, 0.37)	0.21 (0.11, 0.34)
2014	0.82 (0.75, 0.88)	0.83 (0.77, 0.89)	0.25 (0.17, 0.34)	0.24 (0.16, 0.36)
2015	0.77 (0.71, 0.84)	0.80 (0.73, 0.87)	0.33 (0.22, 0.47)	0.37 (0.25, 0.52)
2016	0.87 (0.81, 0.92)	0.88 (0.83, 0.93)	0.33 (0.19, 0.48)	0.35 (0.21, 0.53)
2017	0.74 (0.66, 0.82)	0.72 (0.66, 0.79)	0.24 (0.14, 0.36)	0.17 (0.08, 0.30)
2018	0.78 (0.70, 0.85)	0.79 (0.73, 0.86)	0.34 (0.23, 0.48)	0.31 (0.19, 0.47)
2019	0.84 (0.77, 0.91)	0.85 (0.77, 0.92)	0.23 (0.12, 0.36)	0.21 (0.10, 0.36)
2020	0.87 (0.80, 0.93)	0.87 (0.79, 0.94)	0.27 (0.08, 0.49)	0.24 (0.04, 0.51)
2021	0.75 (0.66, 0.85)	0.72 (0.63, 0.83)	0.21 (0.11, 0.35)	0.16 (0.06, 0.33)
2022	0.87 (0.79, 0.94)	0.88 (0.78, 0.94)	0.26 (0.10, 0.46)	0.24 (0.07, 0.47)

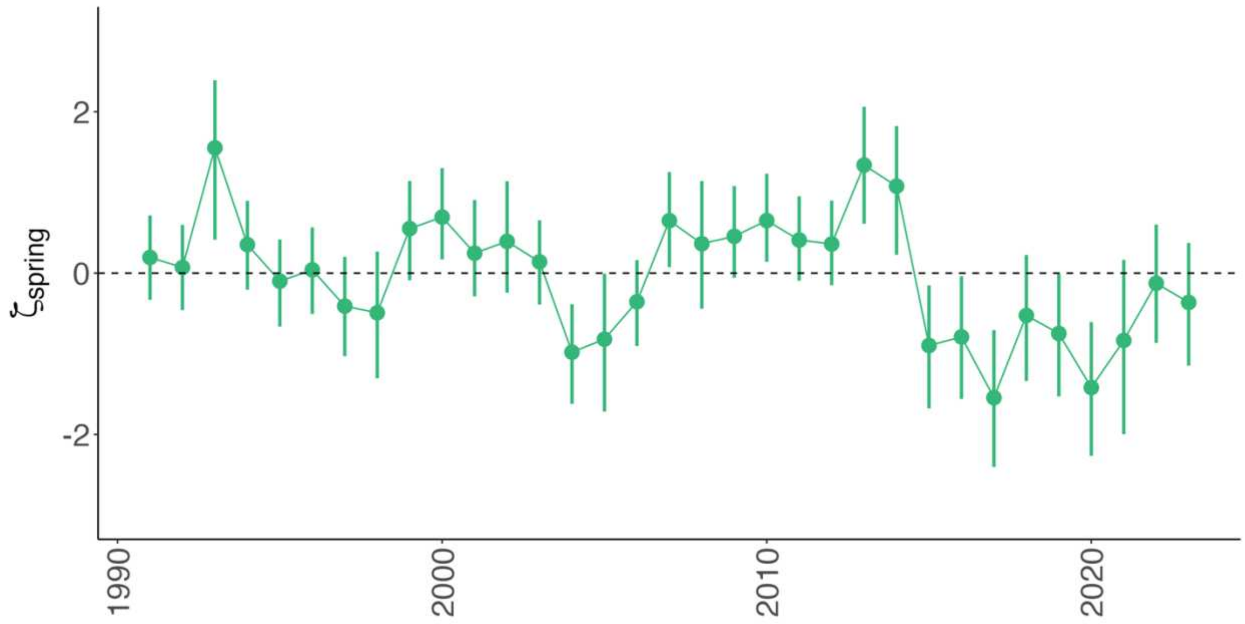
Supplementary Table 1.2: Derived mean survival probability and associated standard deviation (sd) for each age and sex group over the duration of the study

Age-sex group survival (S)	mean	sd
$S_{ad,m}$	0.84	0.05
$S_{ad,f}$	0.85	0.06
$S_{juv,m}$	0.29	0.08
$S_{juv,f}$	0.29	0.10

Chapter 2 Supplementary Materials



Supplementary Figure 2.1: Measured variables of spring timing over time (1990-2023) with median calendar date (CD) of nest initiation at the Tutakoke breeding colony from 1990-2023 (a), calendar date of 10% snow cover at the Tutakoke breeding colony from 1985-2013 (b), and annual average (March-May) spring sea surface temperature (SST) in °C around the Alaska Peninsula from 1990-2023 (c). Long-term linear trendlines are shown in red.



Supplementary Figure 2.2: Estimated posterior mean for annual normalized spring timing (ζ_{spring}), a latent SEM parameter, with 95% Bayesian credible intervals. The horizontal dotted line at y = 0 represents the long-term average date of spring timing.