Thirty Years of Local Semipalmated Plover (*Charadrius semipalmatus*) Population Dynamics in Churchill, Manitoba, Canada: A Long-Term Study on Factors Influencing the Rate of Population Change Over Time

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Abstract

Thirty Years of Local Semipalmated Plover (*Charadrius semipalmatus*) Population Dynamics in Churchill, Manitoba, Canada: A Long-Term Study on Factors Influencing the Rate of Population Change Over Time

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I used 31 years of Semipalmated Plover (*Charadrius semipalmatus*) population data to assess the effects of vital rates on a local breeding population of plovers in Churchill, Manitoba, Canada. I used three similar Bayesian Integrated Population Models (IPMs), with the last a coupled IPM population viability analysis (PVA) approach to predict the impact of changing spring temperatures on future population size. I estimated adult and juvenile apparent survival, fecundity, immigration rate, and yearly population size estimates, and I found that population growth rate was most highly correlated with immigration and adult apparent survival. Moreover, I found that the population remained relatively stationary with a slight decline in recent years. I also found a significant positive effect of spring average daily minimum temperature on juvenile apparent survival. I used this effect to inform my PVA and to evaluate the risk of quasi-extinction for 20 years after the end of the study. I found a low quasi-extinction risk and a greater probability of the population increasing in the next twenty years when informed by predicted spring temperatures from global climate models. My findings suggest some resilience of this species to one effect of climate change and emphasize the importance of continued monitoring to assess if declines in this species will change as multiple threats to their existence in the sub-arctic progress.

Keywords: Semipalmated Plover, population dynamics, integrated population model, Bayesian, population viability, climate change, adult survival rate, juvenile survival rate, nest survival, immigration, fecundity.

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Chapter 1: Introduction

Background

Fundamentally, the field of population ecology is dedicated to examining the change in numbers of organisms over time and space (Krebs 2020). More broadly, population ecologists are interested in what ecological forces, such as interactions with the environment and other organisms, may be driving these changes over varying spatiotemporal scales. Like the fundamental laws of physics, population ecology may be governed by fundamental principles or laws, that act as a foundation for understanding the dynamics of an ecological system at any scale (Turchin 2001, Berryman 2003). However, there has been considerable debate in the literature over whether this is true, with many arguing both for and against the existence of such laws in this field.

Some argue that while there is evidence that these laws exist, the biological world is far too complex for these laws to apply universally and be used to form predictions (Quinn and Dunham 1983, Lawton 1999). Additionally, those opposed to the notion of general laws in ecology often state that the issue with these laws lies in their lack of applicability at multiple scales (Slobodkin 1988), or similarly that they lack universality and are thus invalid (Lockwood 2008).

On the contrary, some refute these qualms with the qualification that it is not necessary for ecological laws to apply universally, and that because they can apply to a wide enough range of conditions, they are valid (Linquist et al. 2016). Moreover, those that subscribe to this perspective point out that even in so-called “hard sciences” such as physics, there are universally accepted laws that also violate the qualifications that many ecologists take issue with (Cooper 1998, Colyvan and Ginzburg 2003). Linquist et al. (2016) provide an excellent review which documents the history behind this issue in more detail and ends with evidence that supports the existence of such laws, or "generalizations", in ecology.

Currently, there is no consensus on the debate, and recently a more moderate viewpoint has also been proposed which stands to bridge the gap in this debate in that ecologists should adopt a pragmatic approach to these laws (Travassos-Britto et al. 2021). Travassos-Britto et al. (2021) present this pragmatic approach under a more flexible framework that these laws are ever changing and context-dependent, and thus do not need to fit into the logical structures of laws accepted in other disciplines such as physics.

So, what are these laws in ecology? There have been multiple variations proposed, most very similar to each other. I find the most clear and logical set of laws to be those proposed by Berryman (2003). These proposed laws break the field of population ecology into five principles that provide a basic theory for the population dynamics analysis that I aim to achieve in this thesis. First, the principle of geometric growth, also often referred to as Malthus' principle, states that "*all populations grow at a constant logarithmic rate unless affected by other forces in their environment*". Berryman (2003) mathematically depicts the *principle of geometric growth* as:

$$\frac{d}{dt}(lnN) = R = const$$

where N is the population size and R is the instantaneous growth rate (Berryman 2003). To account for the other forces in the environment, he further specifies this law with: $R = f(B, G, P)$ where B represents a set of biotic factors such as a population, G their genetic properties, and P the abiotic factors influencing the system. This first principle provides a starting point for understanding ecological systems at increasingly complex levels and is the foundation for all ecological modelling.

The remaining four principles proposed by Berryman (2003) build on this foundation by adding the ecological forces that regulate a population's change over time. His second principle of cooperation states that individuals within a population often gain advantages through increasing population density in terms of survival, reproduction, or instantaneous growth rate (R). This principle also comes with the caveat that there must be an upper limit to population growth as resources become more limited. The *principle of cooperation* can be expressed as:

$$R = A - B\frac{1}{N_{t-d}^{u}} = A\left[1 - \left(\frac{E}{N_{t-d}}\right)^{U}\right]$$

where A is the maximum per-capita rate of change, B is a proportionality constant, E is an equilibrium point (sometimes called an extinction threshold) that the population is generally moving towards, N_{t-d} is the population's density d units of time in the past, and U is a coefficient allowing for non-linear density responses. This principle allows for regulation if a population increases past the equilibrium point such that it will decrease back towards this number.

The third principle is that of competition, which adds an additional layer of complexity in that it acts against the second principle such that populations will have a harder time finding resources and will attract more predators as they grow, resulting in lowered reproduction and/or survival. Berryman depicts the *principle of competition* as:

$$R = A - BN_{t-d}^{Q} = A\left[1 - \left(\frac{N_{t-d}}{K}\right)^{Q}\right]$$

where A and B are the same as the previous equation, K is the equilibrium density, and Q is a coefficient allowing for nonlinear density dependence. These first three principles summarize the within-species dynamics that occur in population ecology.

The fourth and fifth principles differ from the first three because they begin to introduce food web dynamics (i.e., interspecific interactions) into the system. Thus, the fourth is the *principle of interacting species*. This principle is usually incorporated into studies of population dynamics through predator-prey interactions (Ives and Dobson 1987, Vucetich et al. 2011), often depicted through Lotka-Volterra type models (Shim and Fishwick 2008). Berryman (2003) proposed a simplistic set of equations similar to Lotka-Volterra models that assume populations are regulated by predator and prey population densities:

$$R^N = f^N(N_{t-1},P_{t-1})$$

$$R^P = f^P(P_{t-1}, N_{t-1})$$

where R^N and R^P are per-capita rates of change in predators and prey, and f^N and f^P are density functions for predators and prey that can be specified depending on the specific system. Berryman (2003) considers this a general law of population ecology because, while it can be applied to predator-prey dynamics systems, it can also be applied to population dynamics analyses in a more general sense such that any system involving negative feedback (e.g., climate change) on a population can be modelled stemming from these equations.

Finally, the fifth *principle of limiting factors* is a broader overarching principle which aims to recognize the effects of the many feedback loops affecting populations, both by multiple species and physical factors such as resource limitation, genetic factors, and climatic variables. Berryman (2003) states that, if all the potential limiting factors were to act on a population's dynamics, most systems would display chaotic patterns. Because chaotic dynamics are rarely seen in nature, this principle then revolves around the conclusion that there are usually only one or two forces dominating population regulation, leading most often to various cyclical patterns of population dynamics. Berryman concludes his description of this principle with the caveat that the forces behind any system can change at any time, and between locations, leading to intrinsic variability between population dynamics examined at different spatiotemporal scales.

There are many different techniques that have been adopted by ecologists to apply these basic principles to real populations. Depending on factors such as the type of organism, their life history, and the scale of the question being posed, ecologists can choose the method(s) most suited to their population of study. The first basic component of understanding a population focuses on estimating the size of a population and its rate of change over time (Juliano 2007), otherwise known as a population's growth rate. Depending on the question at hand and the organisms involved, these points of time can vary from hours in single-celled organisms (Jafarpour et al. 2018), to thousands of years in species with extremely long generation times such as coast redwood (*Sequoia sempervirens*) (Busing and Fujimori 2005). In its simplest form which ignores factors such as immigration, emigration, and age or sex related differences in survival and reproduction, population growth rate can be defined as: growth rate (λ) = instantaneous birth rate – instantaneous death rate (Sibly and Hone 2002).

Population growth rate can be estimated using population census data (Sibly and Hone 2002) or demographic data such as stage- and sex-specific (i.e., at varying life stages such as juvenile and adult) survival rates, fecundity, immigration, and emigration (Sæther and Bakke 2000). While both methods can yield similar results, depending on characteristics such as population density one may be preferred over the other (Sibly and Hone 2002); thus, when possible it is ideal to integrate both demographic and census data to yield unbiased estimates of population growth rate.

The second basic component to understanding a population's dynamics is exploring the forces that are influencing the change in numbers over time (Juliano 2007). These causal forces quickly begin to incorporate the five laws proposed by Berryman (2003) and are important for population management strategies targeted both for increasing population growth rate (Dinsmore et al. 2010) and for reducing forces acting negatively on population growth rates such as nuisance species (Juliano 2007). Additionally, understanding these forces often leads to more accurate forecasts of population size into the future, which is particularly useful for informing population management strategies of endangered species (Morris et al. 2002). Some of these causal forces include the demographic rates, also called “vital rates” (Frederiksen et al. 2014), previously mentioned (i.e., survival, fecundity, age at maturity, immigration, and emigration). These vital rates act as a proximate explanation for changes in population size and structure, while the ultimate causes for these changes include environmental factors that could be acting on demographic rates such as climate, weather events, disturbance related to predator-prey interactions and/or humans, habitat, and food availability (Frederiksen et al. 2014).

Techniques for modelling population vital rates

Survival

Survival is one of the most frequently estimated vital rates in population ecology as it is one of the main drivers of population change (Pulliam et al. 1992, Schorcht et al. 2009), and in theory is a relatively simple quantity to calculate. This calculation (Kéry and Schaub 2012), only requires counts of the number of individuals C_t alive at the start of the period t and the number that die ($D_{\Delta t}$) over the course of the period Δt to calculate the survival probability (s_t):

$$s_t = \frac{C_t - D_{\Delta t}}{C_t}$$

However, in practise, it is quite difficult to estimate survival probability because of factors including environmental stochasticity, imperfect observation, and the timing and cause of mortality in individuals being difficult to observe (Sandercock 2003, Dennis et al. 2006). There are many ways to estimate the survival of individuals in a population such as maximum longevity records, life-tables, and mark-recapture analyses, some of which can be more useful than others in producing accurate measurements of survival rates in a population (Lebreton et al. 1993, Sandercock 2003).

Although it is subjectively interesting to know the maximum longevity of a species, this method for estimating survival is rarely used, as longevity records are the product of complex relations between survival and recapture probabilities and are also not correlated with survival rate (Krementz et al. 1989). Life-table analyses are another method for estimating survival. These analyses are conducted either by sampling the entire population's age structure at a single point in time or by tracking a cohort over time from birth to death., These methods are not frequently used in ecological studies because of drawbacks including logistical difficulty in collecting the needed data (i.e., requiring stage-structured data), and because survival rates are usually treated as constant across individuals (Murray and Patterson 2006, Molles et al. 2017). Finally, the most common technique for estimating survival are mark-recovery analyses, where members of an open population (i.e., a population that experiences immigration and emigration) are given individually identifiable markers that allow researchers to follow their survival over time.

Depending on factors such as the habits and life history of the organism of interest, the length of study, and the specific goals of the study there are many different variations of the "mark-recovery" technique that can be used to estimate survival rates. Mark-recovery is a general category but depending on the data type (i.e., live recovery, dead recovery, etc.) is also referred to in the literature as: mark-recapture, capture-recapture, dead-recovery, ring-recovery, band-recovery, or tag-recovery (Schaub and Kéry 2022a). Most often, live-recovery methods are employed where apparent survival is estimated over discrete, regular time intervals (i.e., between days, months, years) at which the population is surveyed, and an attempt is made to mark and resight living individuals. *Apparent*, or *local*, survival is used here because it is difficult to differentiate between individuals that have permanently emigrated from the study area and those that have died, although with highly sessile species unlikely to leave the study area *true* survival can be estimated from these data (Sandercock 2006). Thus, these apparent survival analyses produce an estimate of the probability that an individual survives and remains in the study area between time intervals. It is possible to estimate true survival from mark-recapture data, although this requires additional data such as different locations where an individual is observed within the study area (Schaub and Kéry 2022a). Finally, true survival can also be estimated when dead-recovery, or a combination of live- and dead-recovery, data are available.

There are many options for modelling survival using capture-recapture data, with the most commonly used being various formulations of Cormack-Jolly-Seber (CJS) models which quickly became popular among population ecologists after development in the mid-1960's (Cormack 1964, Jolly 1965, Seber 1965, Schaub and Kéry 2022b). CJS models estimate both apparent survival and recapture (or *encounter*) probabilities, and they assume that individuals are observed without error (e.g., flags on individual birds are read correctly), markers are not lost, capture is instantaneous, and captured/recaptured individuals are treated as a random sample of the population (Kéry and Schaub 2012a). These models use encounter history data consisting of 1's and 0's corresponding to whether an individual is encountered (1) or not (0) during each sampling period, and the likelihood of these data is calculated as a product of multinomial distributions whose cell probabilities are functions of survival and encounter probabilities (Gimenez et al. 2007).

There are two ways of estimating likelihood with CJS models, state-space, and multinomial formulations. The state-space formulation is more commonly used, and distinguishes the true ($z_{i,t}$) from the observed state ($y_{i,t}$) of individual *i* at occasion *t* (Schaub and Kéry 2022a). Schaub and Kéry (2022) describe a CJS model as a special case of a general state-space model where the initial state is known, and thus not stochastic, where f_i is the occasion where an individual is first capture and marked. The model likelihood can then be written as:

$$z_{i,f(i)} = 1$$

$$z_{i,t+1} \sim Bernoulli(z_{i,t}\,,\, \phi_{i,t})$$

$$y_{i,t} \sim Bernoulli(z_{i,t}\,,\, p_{i,t})$$

where ϕ is apparent survival probability and p is detection probability.

Conversely, the multinomial formulation of the CJS model is used for a more computationally efficient implementation of this model type, which is most often used with large datasets. In this formulation, capture histories are first aggregated into an array and then parameters are estimated by specifying a product-multinomial likelihood (Schaub and Kéry 2022a). The capture history array, known as an m-array, is assembled by breaking individual capture histories into fragments composed of a release occasion and consequent recapture occasions. Then, the number of fragments is tallied for each sampling occasion, and an additional column in the array is added at the end with the number of individuals released and never observed again. The likelihood is then specified as:

$$\boldsymbol{m_t} \sim \text{multinomial}(\pi_t\,,\, R_t)$$

where $\boldsymbol{m_t}$ is a vector of the t-th row in the m-array, R_t is the number of individuals released at occasion t and π_t is a vector with cell probabilities distributing R_t individuals into $\boldsymbol{m_t}$. The cell probabilities in π_t are the expected frequencies of each fragment of the capture histories and are expressed by functions for apparent survival and recapture probabilities (Schaub and Kéry 2022a). One downside to using the multinomial formulation is that by aggregating individual capture histories into summaries by capture occasion, information pertaining to individuals is lost which can make modelling some effects such as individual heterogeneity impossible. However, it is also possible to assemble and model two or more m-arrays pertaining to groups of individuals that are often of interest such as sex or age groups.

Fecundity

Fecundity is frequently estimated in population ecology and can come in various forms depending on the species and the data available. At its core, fecundity is a measure of reproductive output which can often be broken down and modelled at various stages. In birds, fecundity is a process where the most basic reproductive unit is an egg, of which there a generally more than one in a collection called a clutch laid by a female who, depending on the species, may lay more than one clutch in a breeding season or may not breed at all (i.e., the probability of breeding, or *breeding propensity*). A clutch of eggs may have imperfect hatching success which must be considered, and once a clutch hatches the chicks must survive until they begin flying (until they *fledge*). Thus, individual fecundity in birds can be difficult to model because it is the outcome of several interconnected steps, each with varying degrees of success (Etterson et al. 2011).

Modelling fecundity is often done under two main frameworks, one which involves breaking down the reproductive process into each component and modelling these hierarchically, and another which involves estimating the age-ratio of the population after reproduction (Schaub and Kéry 2022a). The latter approach is not always feasible as it must be possible to age individuals either at a distance, or the data collection method must have an equal likelihood of sampling an individual of any age (e.g., through mist-netting or dead-recoveries from hunting). The former approach can model all or some combination of the previously mentioned stages in the reproductive process, where each stage is modelled with a specific statistical distribution depending on the data type, typically Bernoulli and Poisson models (Schaub and Kéry 2022a).

Immigration

In most ecological population studies, population dynamics are inferred using a combination of the previously described analyses. This approach combines separate analyses of population count, individual survival, and fecundity data to make an informed estimation of changes occurring at the population level. However, this method has a major drawback in that it ignores immigration, a population process that can significantly contribute to changes in the population over time (Millon et al. 2019). In open populations, immigration almost always contributes to population change to some degree (Sandercock and Beissinger 2002), and thus not including this in studies of population dynamics can yield overestimated survival and/or reproductive rates. Additionally, understanding the impact of immigration rates on population dynamics is important because this can help identify whether a population is a source or sink (Peery et al. 2006).

Although it is possible to estimate immigration in studies of population dynamics, this can be difficult as it may require alternative specialized methods in addition to the collection of demographic data including radiotelemetry, removal trapping, exclosures and enclosures, peripheral lines of traps surrounding grids (Nichols and Pollock 1990) or genetic analysis of individuals (Broquet and Petit 2009), some of which may not be possible to use depending on the study species or logistical constraints. As well, methods such as Pollock's robust design (Pollock 1982) have been developed to estimate the contribution of immigration and emigration to additions (births + immigration) and losses (deaths + emigration) in the population size. However, this design also requires a specific sampling method consisting of primary and secondary sampling periods within each major sampling period (i.e., within a year) where the population is assumed to be closed, which again, may also not be logistically possible in many field studies (Nichols and Pollock 1990, Kendall et al. 1997).

Integrated Population Models (IPMs)

Recently, another method that allows for estimating immigration solely through demographic data has become popular in the literature, known as integrated population modelling (Schaub and Abadi 2011). This technique integrates multiple sources of data influencing the overall population dynamics, which can allow for estimation of the immigration rate because all of the other vital rates impacting the population (i.e., births, deaths, emigration) are accounted for (Abadi et al. 2010). However, the usefulness of IPMs extends far beyond just being able to estimate immigration rates.

Schaub and Abadi (2011) define IPMs as models that simultaneously analyse data on both population size and demographic rates, constructing a joint likelihood of two or more datasets which allows for an estimation of population size and the demographic rates that are influencing the population growth (Zipkin and Saunders 2018). This is different from traditional analyses using demographic and population size data in that, instead of creating demographic models separately and combining the demographic rate estimates with a population model (Hitchcock and Gratto-Trevor 1997), IPMs combine these separate piecemeal analyses into one hierarchical model (Besbeas et al. 2005). Some advantages to IPMs over non-integrated analyses are that all available information can be used, uncertainty related to variances and covariances in demographic rates and population growth can formally be accounted for, and all demographic parameters can be considered, which eliminates the bias that some analyses have due to missing demographic information (Schaub and Abadi 2011).

Here, the steps for constructing an IPM outlined in Schaub and Abadi (2011), Schaub and Kéry (2022), and Kéry and Schaub (2012) will be introduced. The first step is to (1) define a population model linking the demographic rates to the overall population size. These are typically matrix models, such as an age-structure model like a Leslie matrix or a stage-structured model such as a Lefkovich matrix. The next step is to (2) define the likelihoods of the individual datasets. Often these are state-space models (SSMs) with equations for both the state process describing how the process of interest (i.e., population growth) changes over time in relation to other parameters (i.e., vital rates), and the observation process which links the true parameter states with the data. The final step is to (3) construct a joint likelihood, which combines the likelihoods of the individual datasets into an integrated model. These steps rely on the assumption that these individual datasets are independent, however it has been shown that for many data types this assumption can be violated as it has little effect on parameter estimates (Abadi et al. 2010).

IPMs can be executed under two main statistical frameworks, frequentist, and Bayesian. The frequentist framework for IPMs, while perhaps more familiar to many ecologists, is more restrictive in that it requires additional assumptions of normality and linearity as well as requiring a technique called Kalman filtering (Besbeas et al. 2002) to maximize the joint likelihood (Schaub and Abadi 2011). Conversely, the Bayesian framework is more flexible because of fewer assumptions, and is also advantageous in that it yields a more logically interpretable outcome in that specific probability statements can be made about parameter estimates (Kéry and Schaub 2012b).

This framework revolves around using Bayes theorem (Bayes 1763), a mathematical theorem which uses probability rules to calculate the probability of parameter estimates given all available information. This information can include both the data and past information on the parameter of interest (Kéry and Schaub 2012b). Kéry and Schaub (2012b) define Bayes' theorem in its simplest form as:

$$p(\theta|D) = \frac{p(D|\theta)p(\theta)}{p(D)}$$

which can be read as: the conditional probability of observing the parameter θ given the data D (the *posterior* distribution) is equal to the conditional probability of the observing D given θ (the *likelihood*) times the marginal probability of θ (the *prior*), all divided by the *marginal* probability of D.

These two frameworks fundamentally differ in that: (1) frequentist inference aims to calculate the probability of the data occurring given a fixed parameter value, whereas Bayesian inference finds the probability of a parameter value in light of the data and all available information, (2) probability in a frequentist framework is defined in terms of infinite relative frequencies of events, while Bayesian probability is defined in terms of the degree of belief the analyst has in an event, (3) frequentist analysis only uses the data collected, while Bayesian analysis can use collected data and prior information, and (4) frequentist frameworks treat parameters as fixed values while Bayesian frameworks treat parameters as random variables (Ellison 2004).

While Bayesian inference is becoming an increasingly popular framework among ecologists, a common argument against the use of this method is that, in addition to being more computationally difficult and thus inaccessible to many scientists, because defining a prior distribution is required in Bayesian analysis, it is impossible to remain objective within this framework. Thus, it can be argued that this is not a scientifically rigorous methodology because of the introduction of subjectivity (Efron 1986). Efron (1986) argues that scientific objectivity is only possible in a frequentist framework. However, this has been refuted by many with the assertion that, even under a frequentist framework, it is impossible for scientists to remain strictly objective as the ideas that are used to generate experiments and hypothesis testing are inherently subjective; thus there is subjectivity involved in any scientific process (Berger and Berry 1988). Additionally, some argue that Bayesian inference is actually more scientifically rigorous because Bayesians explicitly define their assumptions through the use of a prior distribution, while biases in a frequentist framework are essentially hidden from scrutiny (Wagenmakers et al. 2008).

Avian Ecology

Our society is currently facing a global biodiversity crisis, with as many as 10 million species globally facing a current risk of extinction (IPBES 2019). The rate and magnitude of extinction of Earth's species is similar to the five previous mass extinction events in our planet's history, with this being widely considered a sixth mass extinction event, dubbed the "Anthropocene extinction" (Dirzo et al. 2014). The threat of extinction varies among different taxonomic groups; across vertebrates between 16–33% of all species are currently listed as threatened (Hoffmann et al. 2010). In North American avifauna, historical and current records demonstrate losses of roughly 29% of the abundance that was present in 1970 in much of the continent's species, which equates to almost 3 billion birds lost since that time (Rosenberg et al. 2019).

Rosenberg et al.'s (2019) study reporting on the state of North American birds represents a stark warning of the direction populations are trending and identifies specific groups of birds whose trends are most concerning. They identify four different 'management groups' of birds: shorebirds, landbirds, waterbirds, and waterfowl. They reported that all but waterfowl populations have experienced steep declines since 1970. Shorebird populations have experienced the steepest declines among these management groups, with a 37% decline in abundance and two thirds of 44 species experiencing declines (Rosenberg et al. 2019), and recently it has been demonstrated that these declines are accelerating (Smith et al. 2023). Thus, this is a group of birds requiring particular attention by researchers if these trends are to be ameliorated.

There is also considerable diversity within shorebirds, with some groups more at risk of decline than others (Thomas et al. 2006, Galbraith et al. 2014). Some of the shorebirds experiencing the greatest declines are long distance migrants that breed in the Arctic and winter in South America (Thomas et al. 2006), although this pattern has not recently been tested as declines have become more severe. These birds use many habitat types such as coastal beaches, mudflats, and marshes to farmland, forest edges, and wetlands (Burger et al. 1997, Gillespie and Fontaine 2017). Because of the wide range of geographic areas and habitats these birds use throughout their annual cycle, they are exposed to myriad threats on both breeding and non-breeding grounds, in addition to the many threats they face associated with using a relatively small amount of staging habitat during their lengthy migratory routes (Galbraith et al. 2014). These shorebirds are experiencing declines outside of their migration as well for several reasons associated with anthropogenic sources such as habitat loss and alteration, climate change, harvest mortality, disease, and pollution (Reed et al. 2018).

With declines in shorebirds happening at an accelerating rate (Smith et al. 2023) identifying species of concern and attempting to understand what aspect(s) of their annual cycle are driving declines is important. Because of the number of threats they face, this can be a daunting task, as for most species it is very likely that forces causing their declines are happening throughout the annual cycle, not just at one stage. Therefore, it is essential to examine these populations at each stage of the annual cycle (i.e., breeding, non-breeding, and migration), and ideally over a long period of time to identify which issues need to be tackled first to address declines.

Climate change is a threat of major concern with respect to Arctic breeding shorebirds because changes to Arctic ecosystems are already happening (IPCC 2023), and some of the changes occurring are happening faster in the Arctic relative to more southern ecosystems, resulting from positive feedback loops caused by changes in surface albedo and snow cover (Zhang et al. 2013). One aspect of climate change threatening many Arctic ground-nesting species is shrubification which is likely to reduce the amount of available habitat for many species breeding in open habitats (Boelman et al. 2015, Wauchope et al. 2017). The effects of this phenomenon to date are most pronounced at the treeline (i.e., the northern edge of the boreal forest) (Zhang et al. 2013), and are also associated with the treeline advancing northwards, making this an important zone to study the effects of climate change on shorebirds nesting in habitats that will be impacted soonest.

Shrubification and other ecosystem shifts induced by climate change are not a new occurrence, and have been documented for some time (Tape et al. 2006, Zhang et al. 2013, Mekonnen et al. 2021). Thus, to be able to understand the effects these ecosystem shifts have had on shorebird populations, long-term studies are most effective. In Semipalmated Plover (*Charadrius semipalmatus*), one such shorebird population study has been conducted at the treeline in Churchill, Manitoba, Canada for over 30 years. The Churchill study is the longest running shorebird biology study in North America, and it represents an unique opportunity to study the population dynamics of an Arctic shorebird species experiencing declines (Smith et al. 2023) in an area where they are most likely to be impacted by the effects of climate change.

<u>Study Species</u>

Semipalmated Plovers are small, well-camouflaged shorebirds that nest in a variety of open habitats in the North American Arctic and sub-Arctic. They are relatively long-lived, with the current longevity record being at least 18 years old (Williams et al. 2021), although more typically marked birds are observed for 5–6 years (Nol and Blanken 2020). They have a breeding range spanning from the north temperate regions of the Canadian Maritimes on the Atlantic coast, extending west through the Hudson Bay lowlands and much of the sub- and low-Arctic all the way to the Aleutian peninsula on the northern Pacific coast (Nol and Blanken 2020).

These plovers nest on well-drained, sparsely vegetated habitats along coastal beach ridges, and near inland lakes, ponds and rivers, on substrates consisting of small pebbles, sand, dry mud, and tundra, sometimes surrounded by vegetation such as willow (*Salix spp.*), birch (*Betula spp.*), spruce (*Picea spp.*), and tamarack (*Larix laricina*) (Blanken and Nol 1998). Additionally, they can nest near Arctic Tern (*Sterna paradisaea*) colonies, where they have higher nest success than in areas without nesting terns (Nguyen et al. 2003). Semipalmated Plovers often nest solitarily, but they will also nest colonially which tends to be associated with high quality coastal habitats. This pattern of nesting can lead to increased reproductive success when compared with inland nesting birds, possibly due to differences in predator communities between the two habitat types (Armstrong and Nol 1993).

Semipalmated Plover have a very wide migratory and wintering range. They travel south from the sub-Arctic through the Atlantic, Pacific, and central flyways (Nol and Blanken 2020). Many spend their winters along the coasts of the United States, on the Pacific coastline extending south from the State of Oregon, and on the Atlantic coastline extending south from the Commonwealth of Virginia. Interestingly, some Semipalmated Plovers also winter much further south of the United States, with many birds spending their winters in the Caribbean, Central America, and South America, with the southern extent of their wintering range located in Southern Argentina (Nol and Blanken 2020). Semipalmated Plovers are among the most common species of shorebirds in North America, particularly with respect to Arctic nesting species, and up until recently it was thought that the global Semipalmated Plover population was stable or increasing (Morrison et al. 1994, Andres et al. 2013). Newer information suggests that they are among many species of shorebirds that have experienced significant declines over the last approximately 40 years (Smith et al. 2023).

Despite being a relatively well-studied plover (Dinsmore 2019) when compared with many other plover species, we have only recently unveiled evidence of their decline, illustrating the increasing need to update what is known about many aspects of Semipalmated Plover ecology, particularly with respect to population trends. Continent-wide declines could be related to many factors throughout their annual cycle as is seen in other shorebird species, for example, threats on the breeding grounds related to climate change (Ballantyne and Nol 2015), habitat degradation (Swift et al. 2017), shifting predator communities (Lamarre et al. 2017), and increasing abundance of geese (Flemming et al. 2016). Semipalmated Plovers could also be declining due to threats along migratory routes that many other shorebirds are experiencing, such as habitat loss (Iwamura et al. 2013, Wang et al. 2022). These threats are most pronounced in species that congregate at high concentrations during migration (Iwamura et al. 2013), a phenomenon less frequently exhibited by Semipalmated Plover (Nol and Blanken 2020) which suggests that their decline may be unrelated to threats during migration. Finally threats on wintering grounds such as habitat loss (Fernández and Lank 2008), sea level rise, and harvest mortality (Reed et al. 2018) could also be contributing to the decline of this species, although the threats on the wintering grounds for North American shorebirds are poorly known and thus require more study. Therefore, it is not only important to study the entire annual cycle to understand the threats many shorebirds are facing, but also each aspect of their cycle to identify specific threats at a finer scale.

Thesis objectives

I attempt to understand long-term forces driving population dynamics in a breeding population of Semipalmated Plover in Churchill, Manitoba, Canada, and how changes in the local climate may be associated with these dynamics. The specific objectives of my thesis are to: (1) determine if this population has declined since the 1990s, (2) identify the demographic rates that have the greatest influence on local population dynamics, (3) identify if local climate influences population dynamics, and (4) determine if this population will be viable into the future in the face of climate change.

There have been recent declines reported for the global population of Semipalmated Plover (Smith et al. 2023). Therefore, for objective 1 I predicted that I would find a similar decline in the local plover population in Churchill. A previous analysis of the Semipalmated Plover population dynamics in Churchill using the data during 1992–1997 and stage-structured matrix population models identified adult and juvenile survival rates as the main drivers of population dynamics (Badzinski 2000). Thus, I hypothesized that these would continue to be most strongly correlated with changes in the population size. Additionally, Badzinski (2000) speculated that, due to high annual numbers of unbanded birds in the population, that immigration was likely to have a significant influence on population dynamics, however no explicit estimate of immigration was made. Thus, I hypothesized that immigration would also be correlated with population changes. Badzinski (2000) also investigated the influence of local temperature on this population and found no effect on annual survival but did find a correlation between temperature and hatching success. Thus, I hypothesized an effect of spring annual temperature on fecundity. I also hypothesized that spring temperature would have an effect on survival rates as temperature has been demonstrated to have an effect on survival of other shorebird species (van de Pol et al. 2010, Cook et al. 2021), and it is possible that Badzinski (2000) was unable to detect an effect on Churchill's Semipalmated Plovers because of the small sample size in their study.

My findings will provide an updated study on Semipalmated Plover population dynamics considering their recent global declines and put this update in the context of climate change. Additionally, my findings will provide the first explicit estimate of Semipalmated Plover immigration rates and their influence on population dynamics, as well as the first PVA and the first use of IPM techniques for this species. These findings could help inform future decisions related to the global status of this species, and management decisions to ameliorate global declines.

Chapter 2: Methods

Study Site

We collected data annually between 1992-2022, from early-June to mid-August during the breeding season, excluding 2020 due to the COVID-19 pandemic. Within a year, these dates encompass, generally, when birds arrive to the breeding grounds to when most chicks had fledged. We collected data in and around Churchill, Manitoba, Canada (58°45`N, 95°04`W); along approximately 25 km of coastline east of the town, at seven inland sites east of the town, and along approximately 10 km of the Churchill River estuary, beginning in 2018 (Fig. 1).

The Churchill region is located at the treeline, the northern edge of the boreal forest in the transition zone from boreal forest to subarctic tundra ecotones. Churchill is a unique landscape as it represents the furthest north location in Manitoba where this boreal-tundra transitional ecotone exists. The surrounding region comprises subarctic tundra, with true boreal forest only appearing between 30 and 50 km south of the Churchill coastline (Dredge and Dyke 2020). Semipalmated Plovers nest in 'coastal' habitats along Hudson Bay and the Churchill River, characterized by sand, gravel, and muddy substrates near willow (*Salix spp.*) or tundra vegetation, and 'inland' sites characterized by predominantly gravel and sparsely vegetated (*Dryas integrifolia*) substrates surrounded by sparse boreal forest and tundra vegetation.

Figure 2.1. Map of the 20 locations routinely searched for Semipalmated Plover nests near Churchill, MB between 1992-2022. The star indicates the Churchill Northern Studies Centre, one of the regularly searched sites and the location of the field station which served as the home base for research activities.

<u>Population census and fecundity data</u>

We conducted nest searching each year beginning in early June across the Churchill region in ideal habitats such as coastal beaches, inland gravel ridges, or sparsely vegetated tundra habitats. To locate nests, we used knowledge of nest territories from previous years and the birds' behaviour (i.e., broken wing displays that are meant to lead predators away from nests, alarm calls, and head bobbing (Weston 2019)), and we located new territories using these behavioural cues and the observers' knowledge of ideal nesting habitat described above. Of the 20 locations searched between 1992-2022, we searched 14 locations consistently across all years, while the remaining 6 locations represent expanded search effort beginning in 2013, with the most recent area added in 2019.

Once a nest was found, we recorded locations using Garmin GPS units. We also marked nest locations with small rock cairns placed 5-10 m away from the nest, depending on visibility for ease of finding the nest upon return. Upon discovery of each complete nest (i.e., nests with four eggs), we floated at least two eggs using the shorebird egg float method (Liebezeit et al. 2007) to determine the approximate age of the nest and to estimate the hatch date. We typically visited nest sites every 2–5 days during incubation to determine fate, although for more remote sites where this was impossible there may have been periods of roughly two weeks (i.e., 10–14 days) between checks. Upon each nest visit, we examined the eggs for signs of hatch (i.e., starring or pipping), and if no eggs were present before the estimated hatch date, we considered the nest failed. For failed nests we attempted to characterize the cause of failure (e.g., depredation, crushed by humans/wildlife, washed out by a storm), however for 12 years (1993–2002, 2004, and 2020) these data were not available. Additionally, for the 2022 nest survival data, we placed camera traps at nests during incubation such that we often determined fate using photos, allowing us to determine exact hatch or failure dates for each nest.

For models that did not include nest survival, I calculated an estimate of fecundity using the maximum number of offspring in the population each year (i.e., the maximum number of chicks observed at any one time at each successful nest) and the maximum number of broods with a known outcome (i.e., either hatch or failure). Population counts were the total number of occupied nests found in the region, excluding renests.

Banding and resight data

We banded adult Semipalmated Plovers with metal U.S. Geological Survey (USGS) bands, alphanumeric leg flags, and/or Darvic colour bands in unique combinations such that we could uniquely identify individuals in the field. We also banded chicks with metal USGS bands and Darvic colour bands. However, up until 2021 chicks were given brood-specific combinations meaning they were not uniquely identifiable without being recaptured. Starting in 2021 in addition to their brood-specific combinations, I painted uniquely coloured dots using enamel paint on each chick's band such that they were uniquely identifiable without being recaptured. We captured unbanded adults and adults previously banded as chicks (i.e., those with only a brood combination) during incubation using bow nets. In rare cases where bow nets were not usable (i.e., if nests were located too close to shrubs), we used walk-in potter traps for capture. We captured chicks by hand generally shortly after hatch, although for some remote nests where frequent checks were not possible or for nests that were opportunistically discovered after hatch, they may have been captured closer to fledge. Additionally, once chicks had fledged (i.e., began flying) they were too difficult to capture.

To compute apparent survival rates, I created encounter histories from a total of 3420 birds including birds banded both as adults (n = 1359) and juveniles (n = 2061). If a bird was observed, either breeding or otherwise (i.e., no nest was found but a banded bird was resighted), during the field season from June to mid-August then I recorded it as a resight, with each year included as capture/resight occasions during analysis. During each field season, we made a constant effort to search for birds with bands. We paid particular attention during late May and early June when Semipalmated Plovers first arrived on the breeding grounds as they are less tied to specific locations during this time and thus there was a greater probability of finding plovers that choose to nest outside of the typically searched areas. We resighted birds using a combination of binoculars, spotting scopes, and cameras when available (i.e., various DSLR cameras depending on year, and Spypoint Solar Dark trail cameras in 2022).

Climate data

The climate data I used for analysis were the June monthly average minimum temperatures for the Churchill region produced by Environment and Climate Change Canada's Canadian Downscaled Climate Scenarios–Univariate method from CMIP6 (CanDCS-U6) dataset which uses the Coupled Model Intercomparison Project Phase 6 (CMIP6) global climate models (Environment and Climate Change Canada 2023). I used data between 1992–2022 for the base and nest survival IPMs, and 1992–2051 for the PVA IPMs. Monthly mean minimum temperatures for this dataset were the average of each daily minimum temperature estimate for the entire month. The temperature data were the average output of 12 grid cells selected from the model that cover the entire area that we searched annually for nests. These cells were each 6 × 10 km, for a total area of 36 × 20 km (720 km^2) (Figure 2).

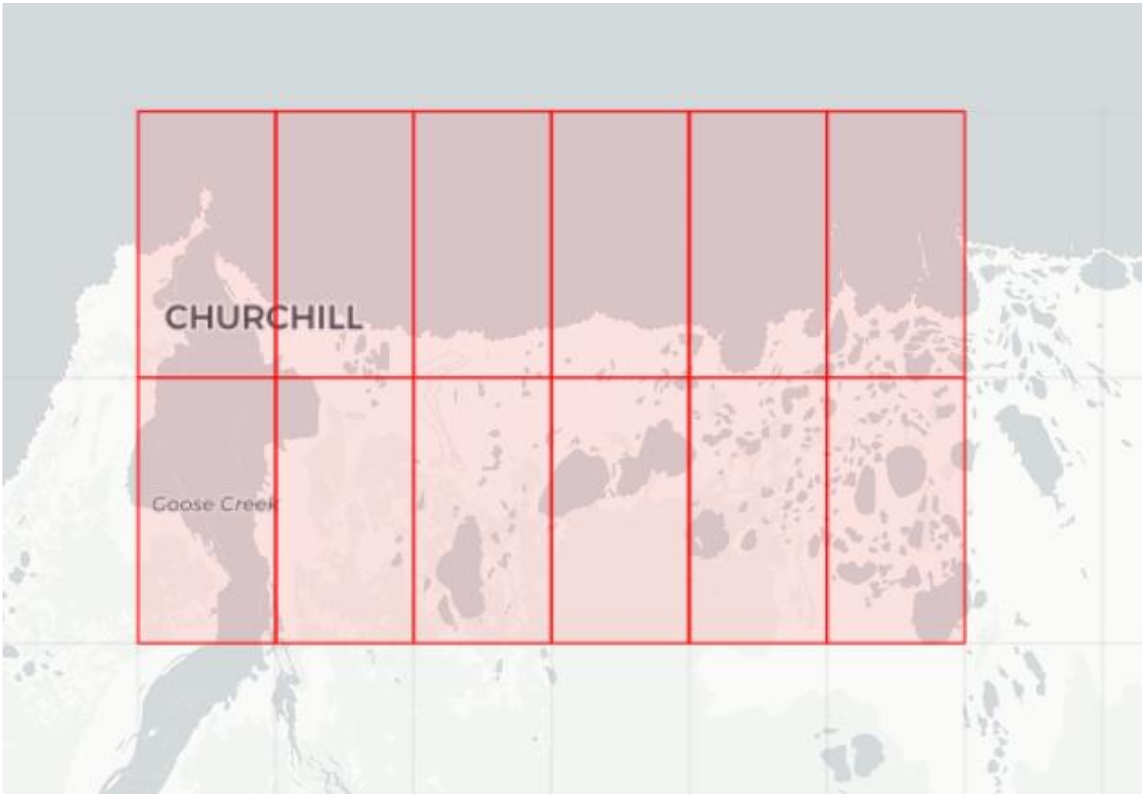

Figure 2.2. Map of the area of the averaged CMIP6 model outputs covering the entire area that was annually surveyed for Semipalmated Plovers near Churchill, Manitoba between 1992-2022. Red cells are 6 × 10 km.

I used output of the CanDCS-U6 dataset for the Churchill region under three different emissions scenarios: SSP 1-2.6, SSP 2-4.5, and SSP 5-8.5. SSP refers to shared socio-economic pathway situations under different political environments and responses to the climate crisis. Under SSP 1-2.6, the least severe emissions scenario available in the CMIP6 model, average global temperature is expected to increase 2°C from the pre-industrial era average by 2100, while under SSP5-8.5, the most severe emissions scenario, the global average temperature in 2100 is projected to be 4.4°C above the pre-industrial average (Meinshausen et al. 2020).

IPM framework

I analyzed IPMs under three similar frameworks, each yielding estimates of population growth, adult and juvenile survival rates, fecundity, and immigration. All models were female-based assuming an even sex ratio, and stage-structured with three sub-models: a state-space model using annual population counts, a mark-recapture model using data from banded adults and chicks, and a fecundity model either using nest survival data or counts of nests with known outcomes (i.e., either hatch or failure) and maximum counts of chicks (i.e., the greatest number of chicks observed for each nest) from each year. I tested the effect of yearly spring minimum temperature as a covariate on juvenile survival, adult survival, and total population size. Then, temperature's effect on juvenile survival was used to inform a PVA predicting all demographic parameters 20 years into the future under three different climate change scenarios.

I structured models assuming a system process with three different classifications of adult birds and an additional inherent juvenile stage. I classified adults as: (N_1) local recruits of age 1 in their first breeding season, (N_{ad}) adults of age 2 or older that have previously bred in the population, and immigrants (N_{im}) breeding in the population for the first time. Although no explicit data were used to estimate the number of immigrants, it can be estimated if all other vital rates in the population are accounted for. However, these estimates of immigration must be interpreted with caution as recent evidence has demonstrated that using IPMs to estimate immigration can yield biased values, especially in cases where there is little yearly variation in the number of immigrants (Paquet et al. 2021). Thus, interpretation of immigration estimates must consider that these values are calculated in part using the residual variation of other model parameters. The juvenile stage (N_0) implicit in the model is dependent on f_t the number of chicks produced per female per year, and the yearly total population size: ($N_0 = \frac{f_t}{2} \cdot [N_{tot,t} = N_{ad,\,t} + N_{1,\,t} +$

$N_{\text{im, t}}$]). Additionally, all system processes within each state-space model incorporate demographic stochasticity by varying as follows:

$$N_{\text{ad},t+1} \sim \text{Poisson}([N_{\text{ad},t} + N_{1,t} + N_{\text{im},t}] \cdot \phi_{\text{ad},t})$$

$$N_{1,t+1} \sim \text{Poisson}(N_{0,t} \cdot \phi_{\text{juv},t})$$

$$N_{\text{im},t+1} \sim \text{Poisson}(\omega_t)$$

where ϕ_{ad} and ϕ_{juv} are adult and juvenile apparent survival probabilities, respectively, from one year to the next whose likelihoods were estimated according to multinomial distributions where encounter histories were aggregated into the m-arrays previously described. Because two age classes (N_1 and N_{ad}) were estimated in these models, two m-arrays were constructed representing each age class that summarized sampling occasions based on individual encounter histories (which were summarized for each sampling occasion as functions of apparent survival probability and encounter probability) and the total number of individuals released at each sampling occasion. The multinomial likelihoods were defined as:

$$\boldsymbol{m\text{-}array}_{\mathbf{juv},\boldsymbol{t}} \sim \text{multinomial}(\pi_{juv,t}, R_{juv,t})$$

$$\boldsymbol{m\text{-}array}_{\mathbf{ad},\boldsymbol{t}} \sim \text{multinomial}(\pi_{ad,t}, R_{ad,t})$$

where π_t is a vector of cell probabilities summarizing survival and encounter probabilities at each sampling occasion and R_t is the number of released individuals on each occasion. The estimated number of breeding pairs in the population was calculated using the observed data and an observation process that incorporates imperfect detection following a Poisson distribution:

$$y_t \sim \text{Poisson}(N_{\text{ad, t}} + N_{\text{1, t}} + N_{\text{im, t}})$$

Where the three different frameworks of IPMs differ is in the estimation of model parameters, specifically with respect to fecundity and apparent adult and juvenile survival. In the first iteration of the IPM, hereafter referred to as the "base" model, I defined fecundity (f_t) as the yearly maximum number of observed juveniles in the population (J_t) following a Poisson distribution constrained by the number of broods (B_t) with known outcomes (i.e., hatch or failure) in each year:

$$J_t \sim \text{Poisson}(f_t \cdot B_t)$$

This is slightly different from traditional analyses of fecundity as, typically, the data used for this are of fledged individuals. Fledging data were sparsely available in this study, so instead the maximum number of chicks observed at each nest site was used for these analyses. Additionally, juvenile survival was calculated for all individuals captured before fledging, so the fledge rate is incorporated into juvenile survival. This means careful comparison between fecundity and juvenile survival rates between this and other studies must be made, as fecundity may be slightly higher and juvenile survival may be slightly lower than what is typically reported. Three formulations of the base model were tested, one with a covariate for spring temperature on juvenile survival, one with covariates for spring temperature on adult and juvenile survival, and one with no covariates.

The second iteration of the model (hereafter referred to as the nest survival model) also explored the effects of a covariate for local spring minimum temperatures on adult and juvenile survival, and fundamentally differs from the base model in that it incorporates an explicit estimation of nest survival into the fecundity parameter estimation such that the number of juveniles in the population (J_t) also follows a Poisson distribution, but differs from the base model distribution as it is constrained by the total observed number of birds in the population in each year (number of pairs multiplied by two), and the daily nest survival rate estimate in each year (dsr_t) calculated using the Mayfield method (Mayfield 1975):

$$J_t \sim \text{Poisson}(2y_t \cdot dsr_t^{30})$$

The purpose of this iteration of the IPM was to break the Semipalmated Plover reproductive process down to a finer resolution to understand the effects that nest survival may have on the overall reproductive output. Ideally, this formulation of the fecundity model would have been used in all iterations of the IPM. However, because daily nest survival data were not recorded in all years the estimation of this process is rather inaccurate and thus was not best for yielding estimates of population dynamics with a higher degree of certainty.

The third iteration of the model, hereafter referred to as the population viability analysis (PVA), is most similar to the first IPM iteration, albeit slightly reformulated to minimize uncertainty such that an accurate prediction of population size into the future can be estimated for 20 years after the final year of the study period. This model also incorporated the effect of a covariate for spring minimum temperature on juvenile apparent survival rates and it reverts to the fecundity estimation method described in the base model due to the amount of uncertainty associated with the nest survival model (because of the multiple years of missing data in this model). It also included a slightly different prior estimation for the immigration parameter. In the first two model formulations, immigration was estimated using a non-informative prior rate that was then converted into the number of immigrants per year, however the PVA IPMs differ in that immigration was estimated using a prior for the expected number of immigrants (i.e., based on the range in the number of unbanded adults observed during data collection), rather than an uninformed rate. The purpose of this immigration parameterization was to prevent overestimation of immigrants (Schaub and Fletcher 2015), which was useful in this case as PVAs inherently include a high degree of uncertainty due to predicting future population sizes with essentially no data.

To make predictions for the PVA model, I augmented the rest of the datasets for the other model parameters with NA values for 20 years into the future, which were then projected during model fitting (Saunders et al. 2018). From these projections, similar to a Piping Plover (*Charadrius melodus*) PVA in Saunders et al. (2018), I calculated the probability that the population would decrease below a quasi-extinction threshold of 10 pairs in the next 20 years, and then I calculated the probability that the population would be smaller in 2042 than in 2022 (the last year data were collected for these analyses).

I fit all models using a Bayesian approach through the program JAGS (Plummer 2003) using the R package jagsUI (Kellner and Meredith 2024), which employs the use of MCMC (Markov chain Monte Carlo) sampling to calculate posterior distributions of the model parameters. Unless otherwise specified, I chose all prior distributions for parameters to be non-informative, although some distributions were truncated to assist with convergence of chains. MCMC sampling was done for 400000 iterations with three chains, a burn in period of 200000 iterations, and a thinning rate of 10 to reduce autocorrelation (Link and Eaton 2012). I visually inspected chains and used the Rhat value to assess model convergence. I only accepted model outputs once convergence was achieved for all parameter estimates. I calculated the derived quantity population growth rate (λ) using model summary outputs by dividing population size in one year by the previous year's population size estimate. I calculated the mean population growth rate as an average of all simulated λ values for each year, and calculated the geometric mean growth rate as one divided by the total number of years multiplied by the sum of log λ for each year.

I assessed model fit and selection using the deviance information criterion (DIC) calculated for each model in JAGS (Abadi et al. 2010), and covariate performance (i.e., I chose models with the lowest DIC values). For models with temperature covariates, I evaluated three candidate models: (1) a global model with temperature covariates for both adult and juvenile survival rates, (2) a model with a temperature covariate only for juvenile survival, and (3) a model without covariates. From these candidate models, only covariates with a significant effect (i.e., covariate values with credible intervals not spanning 0) were included in the nest survival and PVA IPMs.

To assess the effects of vital rates on the population growth rate over time, I calculated correlation coefficients for each vital rate (i.e., adult survival, juvenile survival, fecundity, and immigration) and the population growth rate. This was computed over all posterior estimates between vital rates and population growth rate in each year (n = 60000 simulations per year * 31 years) using the cor() function in the R 'stats' package. Next, I calculated the probability of there being a positive correlation between vital rates and population growth rates by determining the proportion of posterior correlation coefficient estimates that were greater than zero (Kéry and Schaub 2012c). Finally, I calculated the Bayesian credible intervals and posterior modes of all computed correlation coefficients.

Chapter 3: Results

Model Performance

The top performing model according to the DIC was the base model with a temperature covariate included for both adult and juvenile apparent survival rates (Table 3.1, Figure 3.1), although only the juvenile survival covariate had a significant effect. Additionally, the difference in performance between the top performing model and the model without covariates was minimal (ΔDIC = 3.0), and the difference between this and the next best model was even closer (ΔDIC = 1.3). Therefore, I chose to present the results of the model with only a covariate on juvenile survival as the top performing IPM, the most parsimonious model. The nest survival model performed poorer than all three iterations of the base model and the PVA models (ΔDIC = 227.8) (Table 3.1, Figure 3.4). Of the PVA models, which all had a higher DIC than the best overall model, the top performing model was the one with future temperatures derived from a climate model under the intermediate emissions scenario, SSP 4-3.4.

In general, all models yielded similar results, however there were slight differences between each iteration of the models. The results of the nest survival model differed the most from other iterations of the IPMs in that, while the average population growth rate and adult survival rates in this model were similar to those produced in other models, the nest survival model yielded a much lower juvenile survival rate and a much lower immigration rate (Table 3.2) than what was seen in the other model iterations. Additionally, this model differed in having a slightly higher average fecundity than the other iterations of the PVA models, but still lower than the base model. The differences between the nest survival model and other iterations of the IPMs are most telling when comparing Figures 3.3, 3.6, and 3.9, where the population's composition of different demographic groups is shown for each model. Figure 3.6 demonstrates that this model predicted that there was essentially no immigration to the population in Churchill, while the other two figures show between roughly 2 and 27 immigrants joining the population each year.

The average vital rate estimates in the base model were overall similar to those in both the nest survival and PVA models, apart from the fecundity rate which was roughly five times less than that found in the nest survival model, but over triple the rate found in the PVA models.

However, overall population size and growth rate estimates were still similar between the base and other models. Overall, the base model had the lowest amount of uncertainty across all vital rate and population size estimates, and as increasing complexity was added to the model (i.e., estimating nest survival rates, and future population sizes) uncertainty in terms of greater variation in posterior estimates and poorer model performance increased.

Population trends

The Semipalmated Plover population in Churchill, MB has remained, over a 31-year period, stable between 1992–2022. The geometric mean population growth rate across all years in each iteration of the IPMs was roughly 1.01 (95% CI 1.00–1.03), meaning the population was essentially stable with a slight average increase over the entire study period. However, this finding comes with several caveats. First, when examining the trends in the second half of the study period (i.e., 2009–2022), the geometric mean population growth rate in the top performing model was 0.97, suggesting that the population decreased during this period. Additionally, when investigating this decline in the second half of the study period I observed site-specific declines (Table 3.4) at the majority (11/20) of locations searched within the study area. Finally, of the 14 sites that have been searched throughout the study, only 3 had an average increase in the number of nesting pairs, with 11 experiencing declines. Thus, although the models estimated there to be little to no change in population trends over time, it is likely that there have at least been site specific declines, and perhaps a decline in the entire local population, particularly during the second half of the study period.

Despite long-term trends in this study suggesting that the local population of Semipalmated Plovers in Churchill is relatively stable or experiencing slight declines, there is also a very high degree of annual variation in population dynamics that make interpreting the long-term trends more difficult. Over the 31 years of monitoring this population, there was a high amount of variation in the both the observed and estimated number of local nesting pairs each year, with a low of 17 nesting pairs observed in 1992 compared with a high of 68 nesting pairs observed in 2007 (Figure 3.1). Additionally, this high degree of variability was observed more contemporarily, and on a finer timescale, with a relatively high number of nesting pairs observed in 2019 (54 pairs) compared with a relatively low number found in 2021 (26 pairs). This variability can also be seen when examining the average posterior estimates of population growth rate by year, with the greatest growth rate of 1.88 occurring between 1992-93, and the lowest growth rate of 0.61 occurring between 2019–2020. Also, of the 30 population growth rate estimates, 17 represent increases in population size between years (i.e., $\lambda > 1$) while 13 represent decreases in population size between years (i.e., $\lambda < 1$).

Effects of vital rates on population growth

In the top performing IPM, the vital rate that was most strongly correlated with population growth rate was immigration (r = 0.85, 95% CRI 0.35 to 0.92) with a 0.99 probability of a positive correlation (Figure 3.2). The vital rate that was next most strongly correlated with population growth rate was adult apparent survival, with a 0.98 probability of a positive correlation. The other two vital rates that were tested, juvenile apparent survival and fecundity, had a substantially lower probability of being positively correlated with population growth rate. Fecundity and juvenile apparent survival likely had no correlation with population growth, with a 0.41 probability of a positive correlation (r = -0.05, 95% CRI -0.26 to 0.21), and a 0.31 probability of a positive correlation (r = -0.09, 95% CRI -0.28 to 0.20), respectively.

In the IPM that included a measure of nest survival in the fecundity calculations, the effects of vital rates contrast with those from the top performing model that does not include a measure of nest survival (Figure 3.5). In contrast to the top IPM, this model formulation found that juvenile apparent survival was most strongly correlated with population growth rate ($r = 0.58$, 95% CRI 0.25 to 0.75) with a 0.99 probability of a positive correlation, followed by adult apparent survival ($r = 0.46$, 95% CRI 0.19 to 0.63) with a 0.99 probability of a positive correlation, nest survival ($r = 0.18$, 95% CRI -0.08 to 0.39) with an 0.87 chance of a positive correlation, and finally immigration ($r = -0.002$, 95% CRI -0.29 to 0.33) which had a 0.50 probability of a positive correlation. However, this model had much more uncertainty than the top performing IPM due to multiple years where nest survival data were unavailable.

The contrasting effects of the vital rates between the top performing IPM and the IPM that included a measure of nest survival are best observed when comparing Figures 3.3 and 3.6, which present the contributions of surviving adults, local recruits, and immigrants to the population in each year. Figure 3.3 clearly shows spikes and dips in the population coinciding with a greater contribution of surviving adults and immigrants to the population, while very few recruits join the population in most years. In contrast to this, Figure 3.6 shows essentially no contribution of immigration to the population, while surviving adults have a similar contribution to Figure 3.3 and local recruits contribute more to the population over the entire study period.

Effect of spring temperature

In the top performing IPM, Churchill's average spring daily minimum air temperature was correlated with juvenile apparent survival ($\beta_{juv} = 0.394 \pm 0.24$ SD) (Table 3.4). There was no significant effect of average spring daily minimum air temperature on adult apparent survival ($\beta_{ad} = -0.09 \pm 0.36$ SD), and thus this covariate was not included in what I considered the top performing model. Additionally, in each of the PVA models, there was a significant positive effect of the past and projected future temperatures on juvenile apparent survival, with β_{juv} values similar to the top performing IPM (Table 3.4).

Population viability analyses

All population viability analyses under the three differing climate change scenarios produced similar results, with only slight differences in model performance and future population predictions. Nevertheless, the IPM using temperature data from the intermediate climate change scenario tested, SSP 4-3.4, performed slightly better than the other scenarios (Table 3.1) and thus I chose to present the results of this model in Figures 3.7-3.9. Figure 3.7 shows the posterior estimates of population size for the entire 51 years (31 years of study plus 20 years projected into the future). The 31 years of the study produce essentially identical population size estimates to the base model, with fluctuations between roughly 20 and 60 pairs in the population. The 20 simulated years into the future do not differ drastically from this range, however there is a predicted increase in the population over this time from roughly 38 pairs in year 31 (2022) to 65 pairs in the final year (2042). Figure 3.8 shows adult and juvenile apparent survival, fecundity, and immigration over the 51 years, with all vital rates except juvenile apparent survival stabilizing for the 20 simulated years of the study. In this period, juvenile survival increases slightly over time as the climate is projected to warm (Figure 3.10). This trend is best observed in Figure 3.9, which shows local recruits contributing considerably more to the population in the 20 simulated years when compared with the first 31 years of the study period.

In all three population viability analyses, there was a very low probability of the population crossing a quasi-extinction threshold of 10 pairs within the next 20 years. Figure 3.10, which shows the percentage of simulations that cross this threshold over the 20 simulated years, demonstrates that only between 0.1–0.5% of all simulations (n = 60000) in each PVA model cross this threshold, and thus there is a low likelihood of quasi-extinction of this population in the next 20 years. In fact, Figure 3.12, which shows the proportion of simulations where the population increases from the average posterior estimate in year 31 (38 pairs), demonstrates that the population is more likely to increase in the next 20 years. By year 35, all three PVAs predict a greater than 50% probability of the population increasing in the future, and by the end of the 50 years almost 75% of the simulations predict an increase in the population.

When comparing the average posterior estimates of overall population size between the three PVA scenarios, there are no real differences between estimates for the first 31 years of study, however there are slight differences in the 20 simulated years. All three scenarios predict the population to increase in this period, with the intermediate severity climate change scenario (SSP 4-3.4) showing the strongest increase in population size, up to about 65 pairs in 2042. The most severe scenario (SSP 5-8.5) shows an increase to roughly 63 pairs by 2042, and the least severe scenario predicts the weakest increase of the three scenarios, to roughly 61 pairs in 2042.

Summary of 31 years of banding data

A total of 1359 adults and 2061 chicks were banded between 1992–2022 (Table 3.3), with 52.4% of the birds banded as adults returning to breed in the study area at least once. The birds that were banded as adults that returned to the study area in another year were resighted an average of 3.2 times, and a maximum of 10 times, with one individual reaching at least 12 years of age in the last year it was observed. Of the 2061 chicks banded, 3.2% (Table 3.3) returned to the study area to breed at least once. The birds banded as chicks that returned to the study area were resighted an average of 2.7 times, and a maximum of 6 times, with one individual reaching 8 years of age.

Table 3.1. Model performance using deviance, DIC, and pD.

	Deviance	**DIC**	**pD**
Base	2057.3	2167.8	110.5
Base.1 (temp + $\beta \cdot \phi_{juv}$)	2056.2	2166.1	109.9
Base.2 (temp + $\beta \cdot \phi_{ad}$, $\beta \cdot \phi_{juv}$)	2055.7	2164.8	109.1
Nest survival (temp + $\beta \cdot \phi_{juv}$)	2221.5	2392.6	171.1
PVA (SSP 1-2.6)	2058.5	2166.2	107.7
PVA (SSP 4-3.4)	2058.7	2165.1	106.5
PVA (SSP 5-8.5)	2058.6	2166.3	107.7

Table 3.2. Overview of different model iterations. Compares average vital rate estimates calculated over all simulations (n = 60000) and years. For the base model only the results of the best performing model are included.

*Immigration estimate in the PVA models is the estimated number of individuals immigrating into the population rather than the immigration rate

** Fecundity estimate in the Nest Survival model is the nest survival rate rather than true fecundity

	Population growth rate (λ)	**Adult survival (ϕ_a)**	**Juvenile survival (ϕ_j)**	**Fecundity (*f*)**	**Immigration (ω)**
Base.1	1.02	0.740	0.073	2.02	0.22
Nest survival	1.01	0.731	0.016	0.823**	0.05
PVA (1-2.6)	1.02	0.735	0.081	2.02	2.00*
PVA (4-3.4)	1.02	0.735	0.084	2.02	2.01*
PVA (5-8.5)	1.02	0.735	0.081	2.02	2.00*

Table 3.3. Summary of the number of birds captured as adults and chicks in Churchill, MB between 1992-2022, their return rates, and the maximum age reached for each.

	Adults	**Chicks**
Total Individuals Banded	1359	2061
# that returned 1+ times	712	65
Return rate (%)	52.4	3.2
Oldest bird (years)	12	8

Table 3.4. Posterior average and Bayesian 95% credible intervals in parentheses of the effect of temperature covariate(s) and future temperature covariate(s) from all MCMC simulations on all models, excluding the base model run without any covariates.

	$\beta \cdot \phi_{juv}$	$\beta \cdot \phi_{ad}$
Base.1	0.394 (-0.08, 0.89)	—
Base.2	0.394 (-0.07, 0.86)	-0.09 (-0.77, 0.63)
Nest Survival	0.222 (-0.36, 0.81)	—
PVA (SSP 1-2.6)	0.380 (-0.07, 0.85)	—
PVA (SSP 4-3.4)	0.396 (-0.08, 0.85)	—
PVA (SSP 5-8.5)	0.308 (-0.16, 0.73)	—

Table 3.5. Average number of nesting pairs by site for the first (1992-2007) and second (2008-2022) halves of the study period. Some sites were only searched in the later years of the study, as indicated. For sites that were not searched in all years, the average number of nesting pairs since the first year it was searched was calculated. PR site experienced a very minor decrease not seen due to rounding. See Appendix 4 for full site names.

Site	**1992-2007**	**2008-2022**	**Avg since first search**	**+ or -**	**Comments**
WE		3.64	12.75	+	New search area (2018)
TL	1.87	2.07		+	
GB	2.67	5.64		+	Expanded search area
HP	7.53	2.71		-	
EP		1.50	2.33	+	New search area (2013)
EE		2.43	3.78	+	New search area (2013)
FL		0.14	0.67	+	New search area (2019)
LL	3.13	3.43		+	
OC	0.80	0.21		-	
CNSC	0.33	0.00		-	
HT		0.14	0.18	+	New area not searched every year
PR	2.93	2.93		-	Very slight decrease
MP	11.87	5.71		-	
ER		3.07	8.60	+	New search area (2017)
DB	1.53	1.21		-	
MD	0.33	0.00		-	
IB	2.80	0.86		-	
AK	1.20	0.00		-	
BC	3.93	3.57		-	
MISC	2.53	0.79		-	

Base model

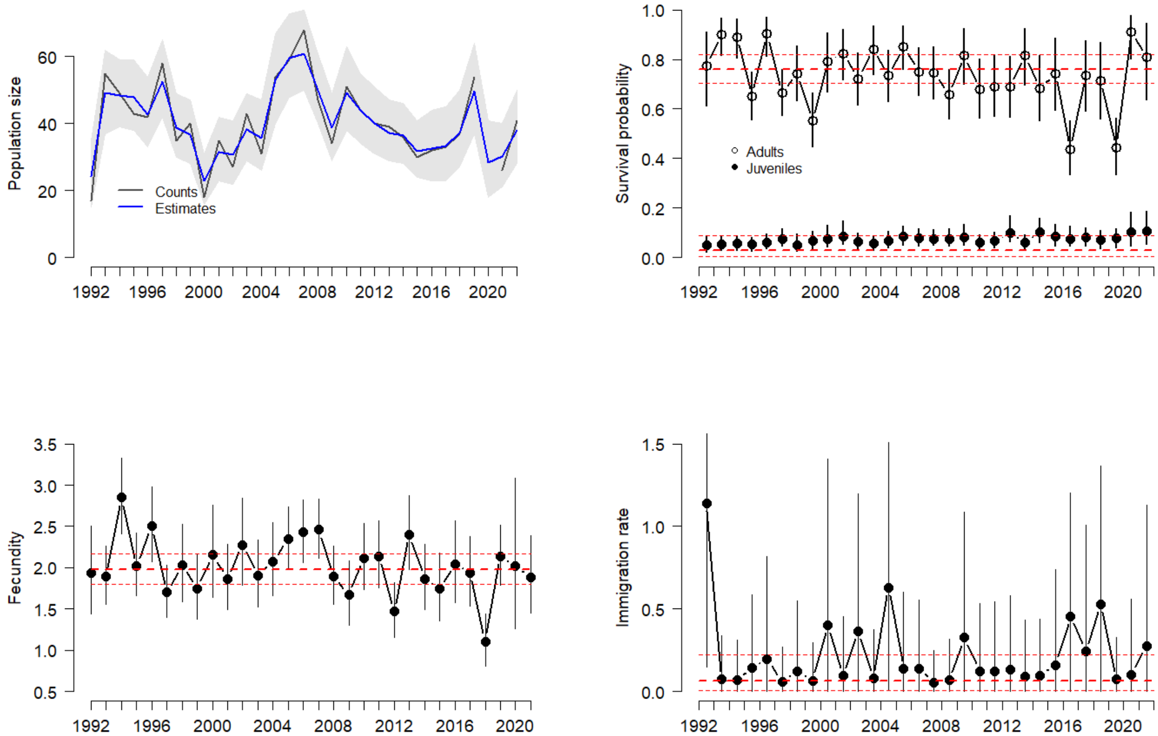

Figure 3.1. Yearly estimates of population size, survival probability, fecundity, and immigration rates from 1992-2022 in the base.1 model. Gray shading on the population estimate graph depicts 95% Bayesian CRI, and red lines on the survival, fecundity, and immigration graphs depicts the mean and 95% quantiles of the hyperparameters for each respective parameter.

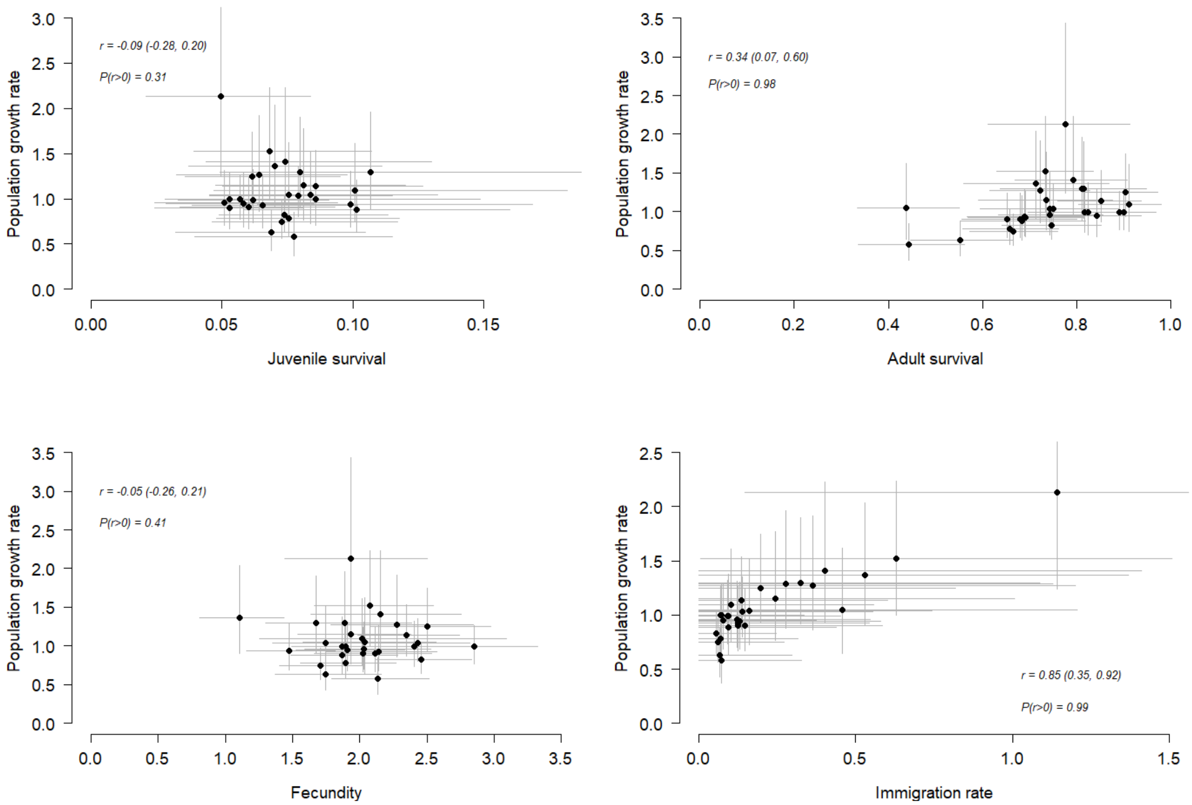

Figure 3.2. Correlation coefficients from the base model between population growth rate and juvenile survival, adult survival, fecundity, and immigration rate. r value on graph represents the posterior mode of the correlation coefficients, and the 95% credible interval, between population growth rate and other vital rates and P represents the probability of a positive correlation between growth rate and each vital rate.

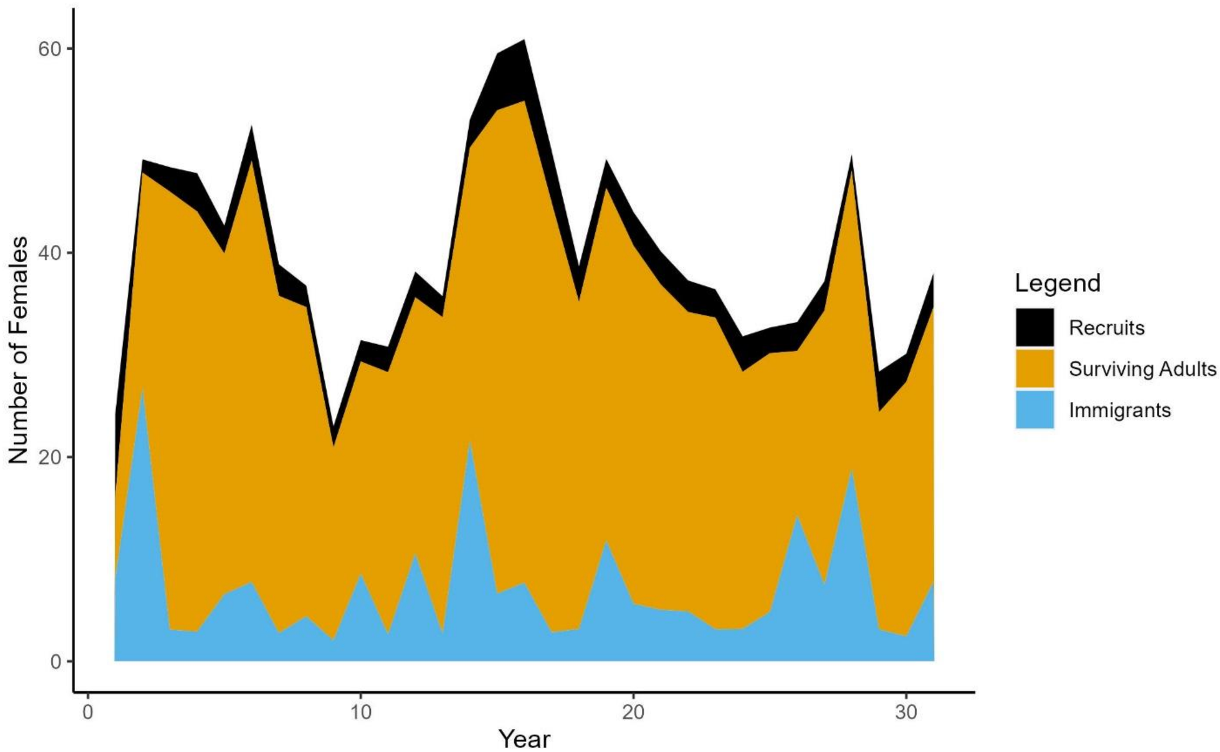

Figure 3.3. Composition of the mean posterior estimates of the total number of female local recruits, surviving adults, and immigrants in the population each year from the base.1 model.

<u>Nest survival model</u>

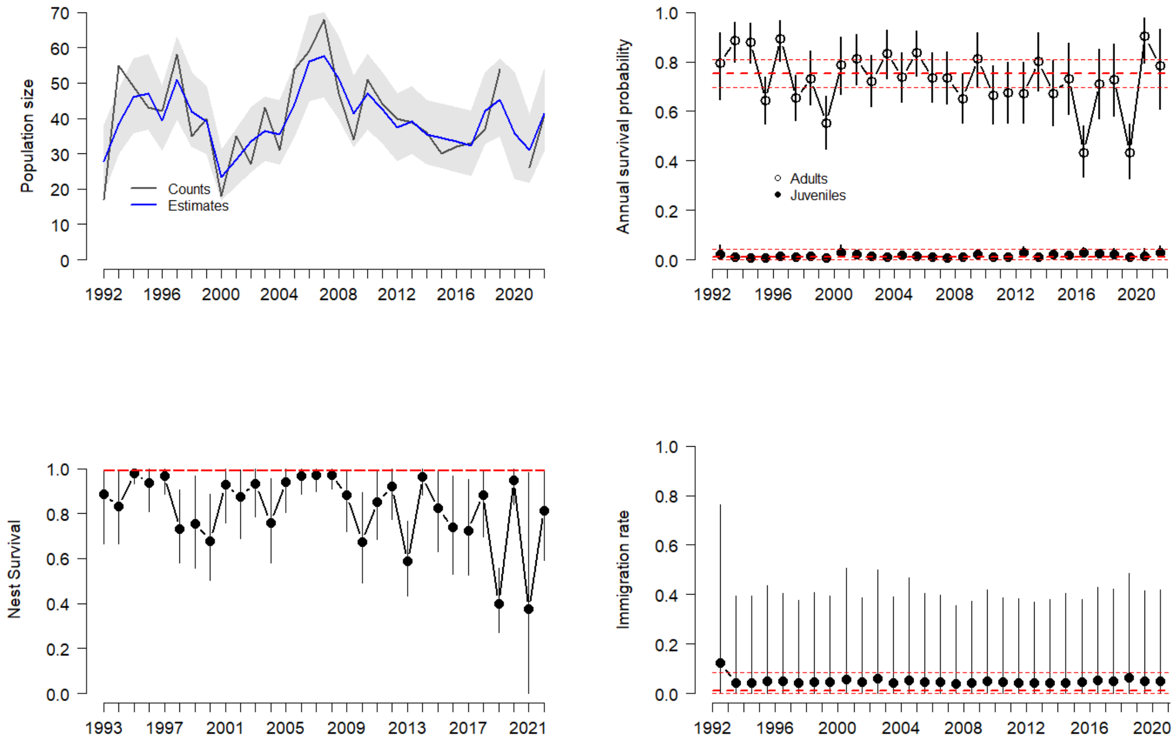

Figure 3.4. Yearly estimates of population size, survival probability, nest survival, and immigration rates from 1992-2022 in the nest survival model. Gray shading on the population estimate graph depicts 95% Bayesian CRI, and red lines on the survival, fecundity, and immigration graphs depicts the mean and 95% quantiles of the hyperparameters for each respective parameter.

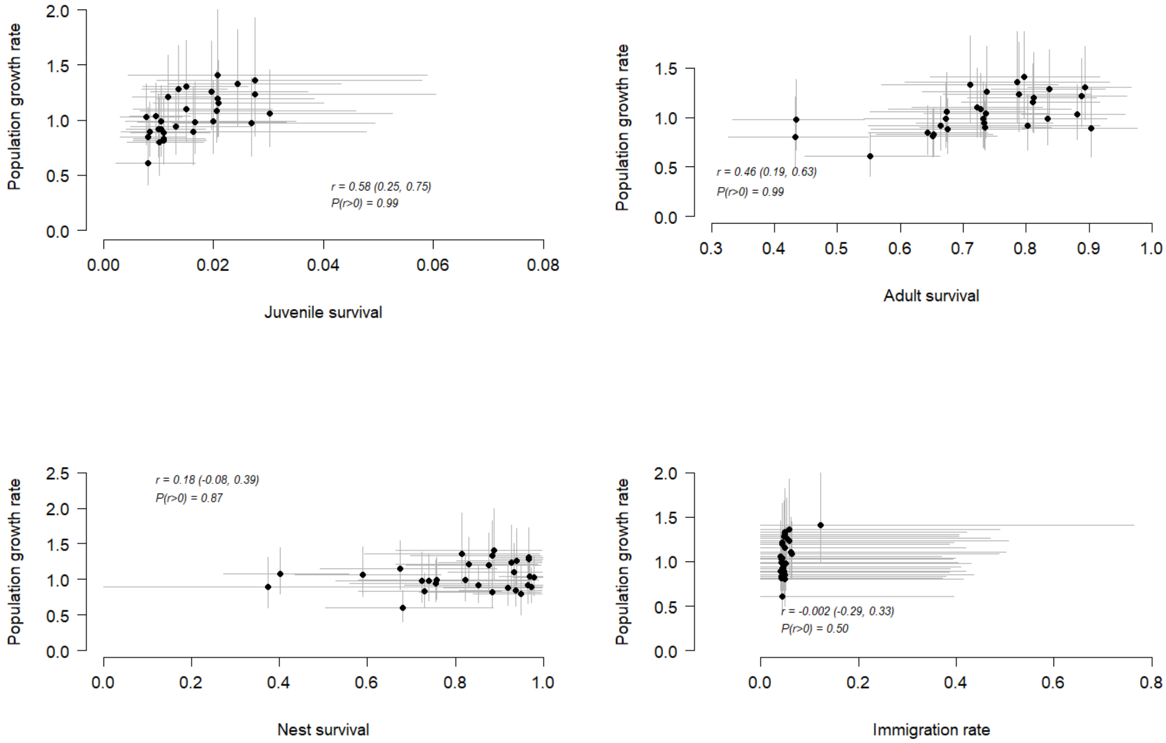

Figure 3.5. Correlation coefficients from the nest survival model between population growth rate and juvenile survival, adult survival, fecundity, and immigration rate. r value on graph represents the posterior mode of the correlation coefficients, and the 95% credible interval, between population growth rate and other vital rates and P represents the probability of a positive correlation between growth rate and each vital rate.

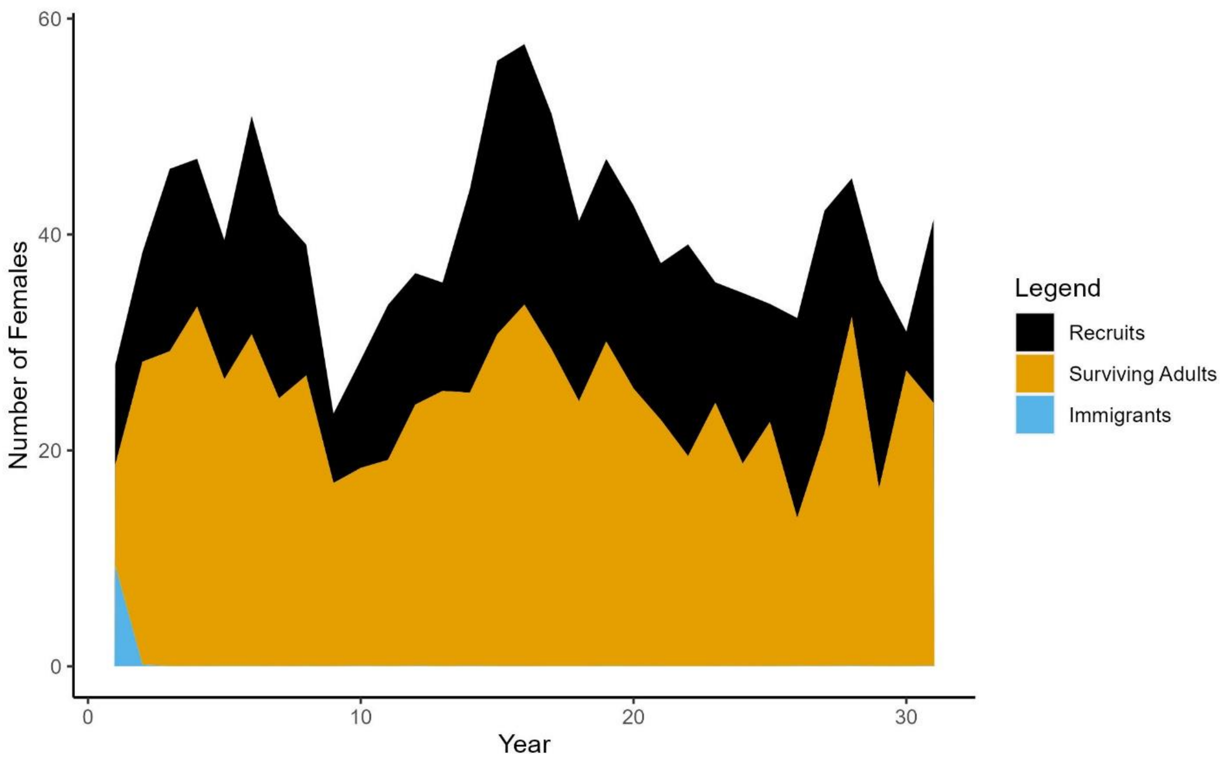

Figure 3.6. Composition of the mean posterior estimates of the total number of female local recruits, surviving adults, and immigrants in the population each year from the nest survival model.

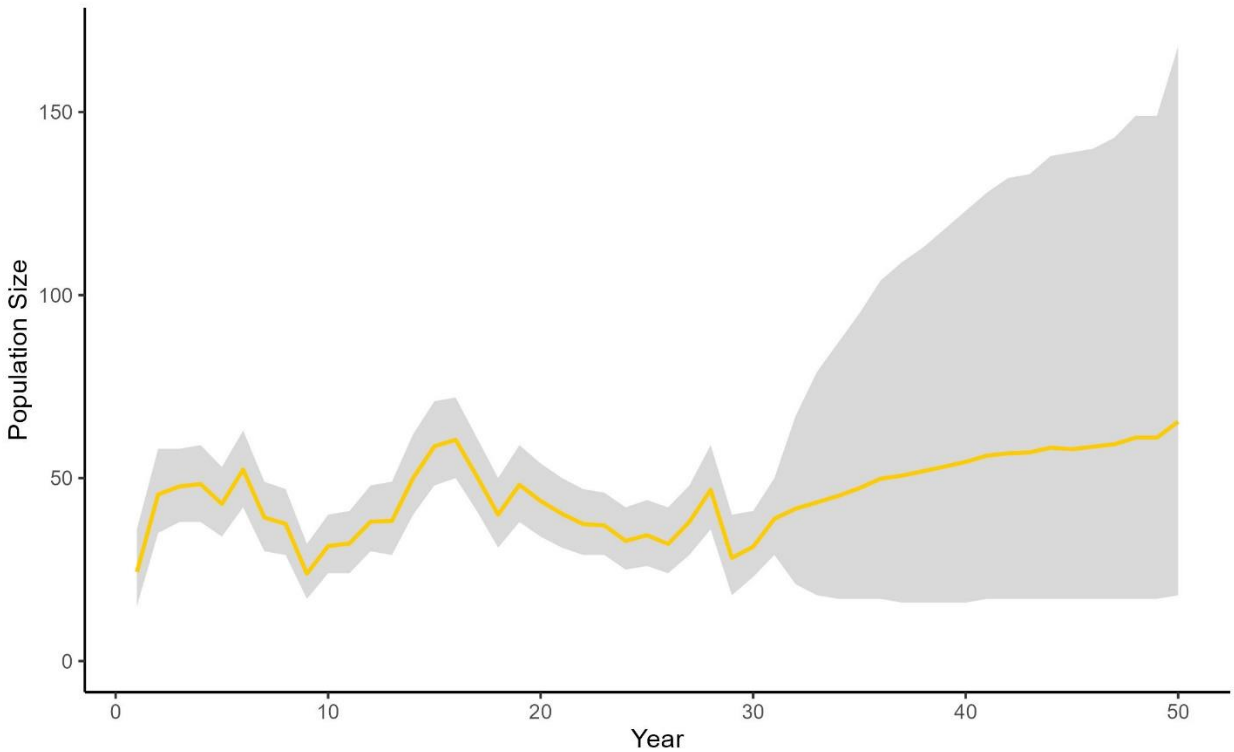

Figure 3.7. Estimated population size for the PVA model under the intermediate severity emissions scenario (SSP 4-3.4). Population estimates after year 30 are based on projected future population vital rates and future temperatures estimated by the climate model.

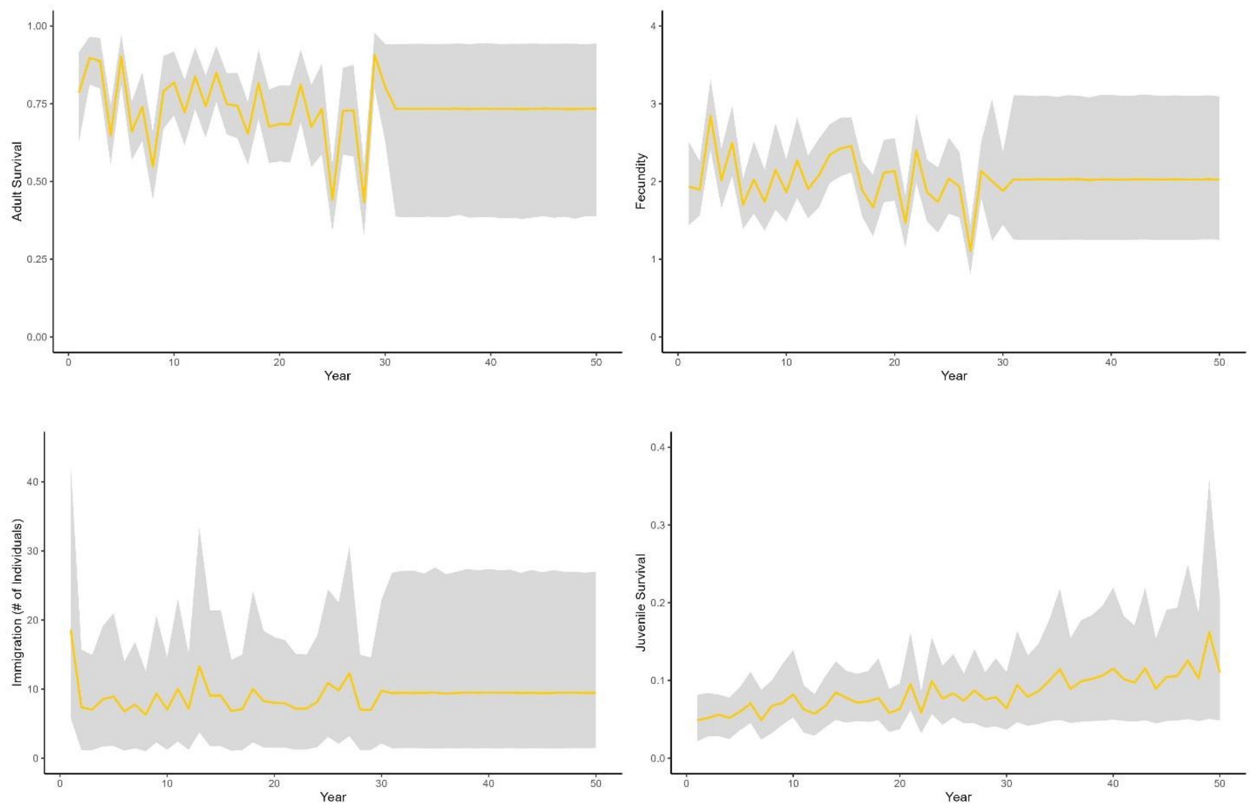

Figure 3.8. Vital rate estimates for PVA model under the intermediate severity emissions scenario (SSP 4-3.4). Estimates from year 31-50 represent future predictions of vital rates informed using the climate model.

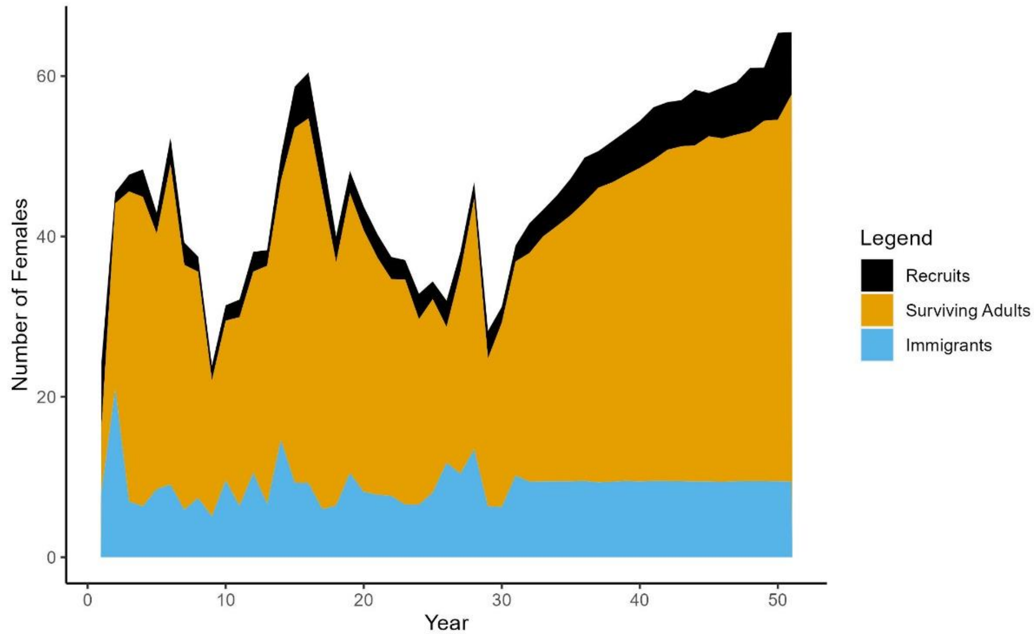

Figure 3.9. Composition of the mean posterior estimates of the total number of female local recruits, surviving adults, and immigrants in the population each year from the intermediate severity emissions scenario (SSP 4-3.4) PVA model.

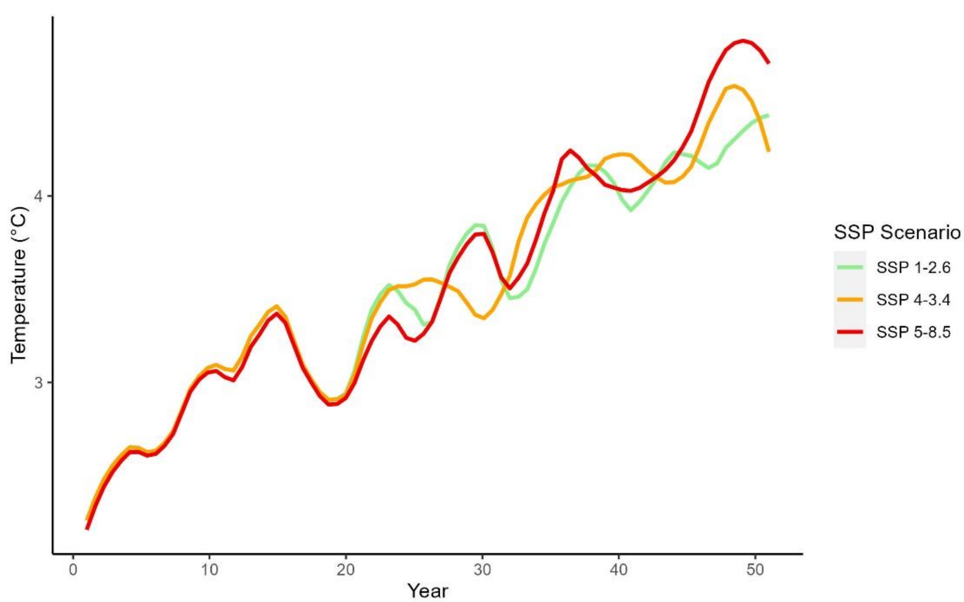

Figure 3.10. Comparison of temperature predictions from the CanDCS-U6 dataset CMIP6 model under three SSP scenarios, smoothed using the LOESS method in the ggplot2 Rstudio package.

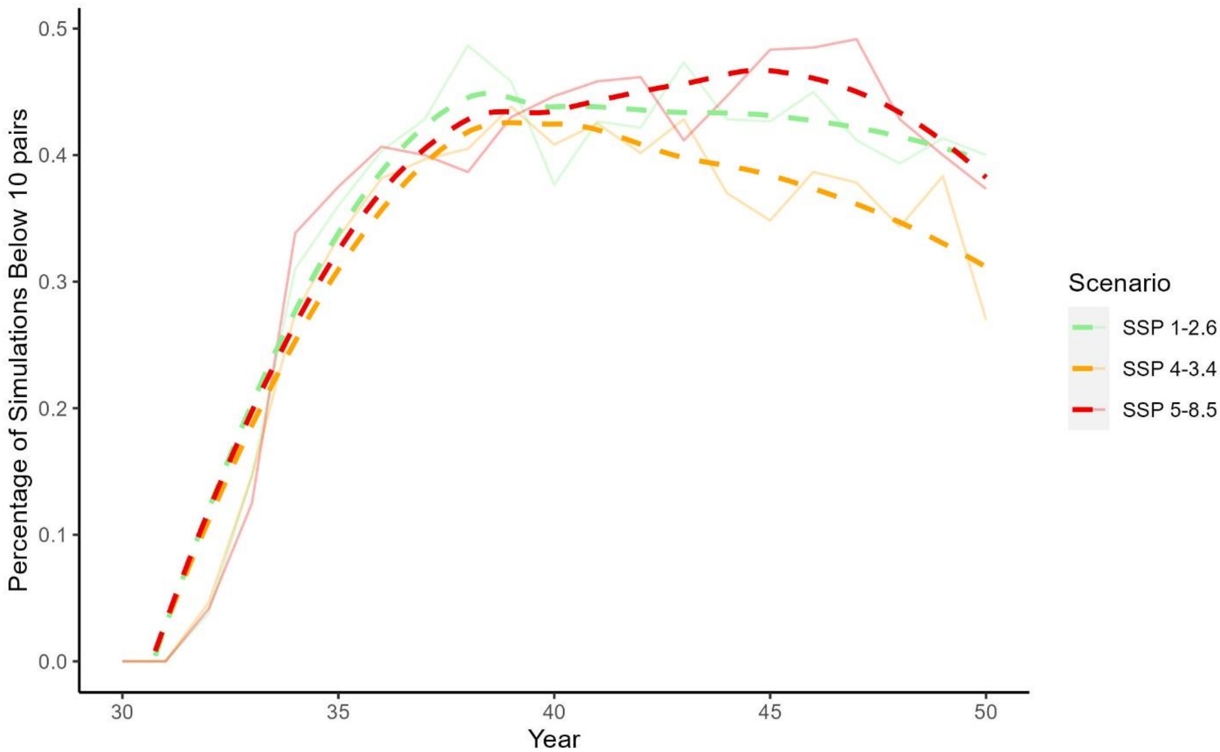

Figure 3.11. Comparison of quasi-extinction probability between the three SSP scenario model iterations. Solid lines represent the true percentages (y-axis range 0.0-0.5%) in each simulated year and dashed lines represent these data with a LOESS smoothing function computed using ggplot2.

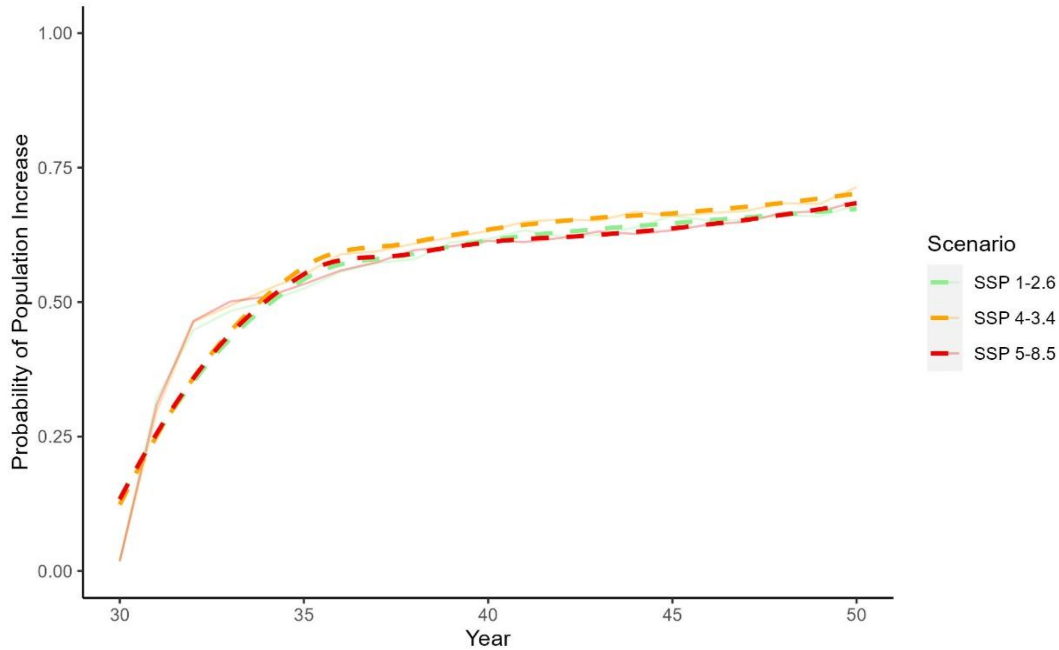

Figure 3.12. Comparison of the probability of the Churchill, MB Semipalmated Plover population increasing under three different SSP scenarios.

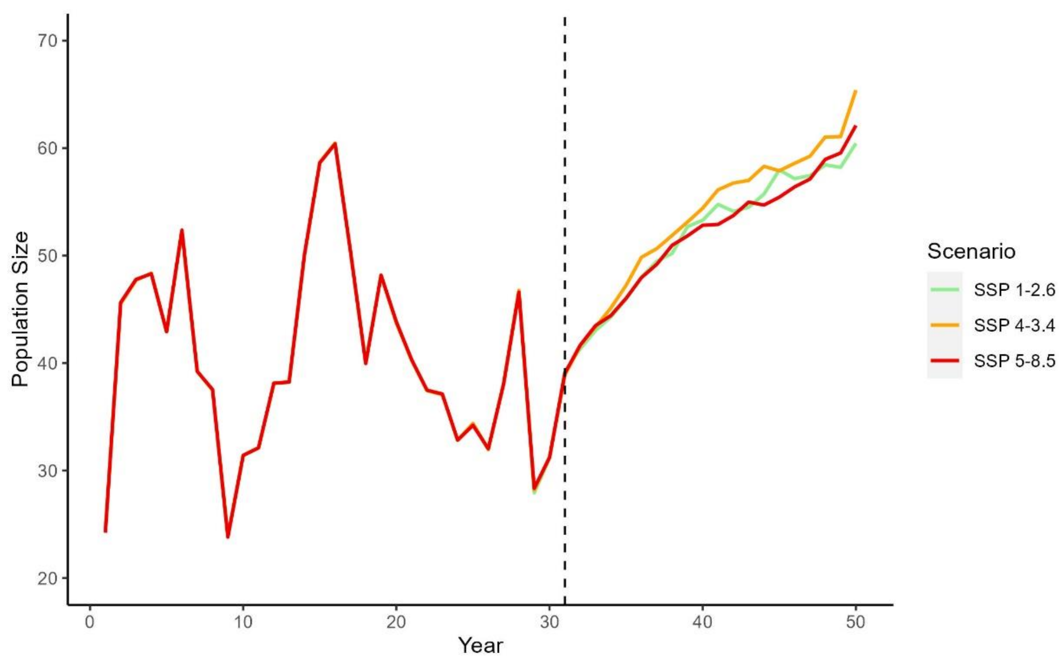

Figure 3.13. Comparison of mean posterior estimates for population size in the three different PVA models under differing climate change scenarios.

Chapter 4: Discussion

My study provides a novel update on what is known about Semipalmated Plover population dynamics at a sub-Arctic breeding site using Bayesian IPMs and a coupled Bayesian IPM-PVA approach. Also, my study provides the first estimates of both immigration and fecundity rates for this species. I tested three different IPMs and the best supported suggests that the population remained stable over 31 years, although stability was maintained through immigration of 2–27 birds annually, likely juvenile dispersers from other populations. I also show high interannual variability in population dynamics, some of which can be explained by warming spring temperatures. Additionally, there was a decline in total population size during the second half of the study period, and site-specific declines at 11 out of 20 sites during this period.

These annual changes in population size were primarily driven by the immigration of new individuals into the population and surviving adults returning to breed year after year. While juvenile survival rates were not a main driver of population dynamics, there was a significant effect of average spring minimum daily temperatures on juvenile survival rates, which resulted in a slight increase in this vital rate during the study period as spring temperatures were warming and are predicted to warm further. The findings of my population viability analyses, informed by future temperature predictions from global climate models and temperature's effect on juvenile survival, suggest a low probability of quasi-extinction for this population in the next 20 years. Although there is a high degree of uncertainty in the future population predictions, I found that the Churchill Semipalmated Plover population has a higher probability of increase than decrease in the next twenty years. My findings suggest that there is some resiliency of this species to the effects of climate change. However, due to the high degree of interannual variability in their population dynamics there is still much uncertainty in these predictions which could result in unanticipated changes to this population's size and structure.

Population trends

I successfully obtained estimates of population growth rates (λ) using IPMs for each of the 31 years that Semipalmated Plover were studied at Churchill, MB, and obtained an average growth rate estimate for the entire study period. The average growth rate for the entire study period was 1.01, suggesting that there was little change in the overall population size throughout the study period. This finding contradicts my prediction that the Churchill Semipalmated Plover population would experience similar declines to those that were reported by Smith et al. (2023), although other trends observed within the population may still indicate a slight decline. Specifically, when observing site-specific trends in the number of nesting birds throughout the study, most (11/20) sites had fewer birds nesting in the second half of the period. This, combined with the fact that the geometric mean population growth rate found during the second half of the study period was 0.97, and that search effort expanded during this time, is evidence that the population in Churchill has experienced a decline. Because immigration and adult apparent survival were the two vital rates most highly correlated with population growth rate, it can be assumed that any decline is likely to be most related to these rates. Because adult apparent survival is influenced by variability in an individual's likelihood to breed in a given year, and immigration is used to estimate changes in population size not reflected in changes to other rates, both vital rates are highly correlated with the number of breeding pairs in the population in each year, and thus any factors influencing the likelihood of a plover either returning to or joining the breeding population should be investigated.

Several threats that many species of shorebird experience during their annual cycle could be contributing to this decline. Outside of the breeding season, threats contributing to shorebird declines include habitat loss (Iwamura et al. 2013), sea level rise (Galbraith et al. 2002), and harvesting mortality (Reed et al. 2018). While these threats are not all exclusive to the non-breeding season, some are less likely to be having significant impacts on Semipalmated Plover during their migratory and wintering cycles as they generally do not congregate in high numbers to the degree that many other shorebird species do (Nol and Blanken 2020), and thus their risk of being impacted by these threats is lowered by being spread over a larger geographic area. Therefore, it seems likely that local population declines in Churchill are related to threats during the breeding season.

Due to the location of Churchill at the treeline where, boreal forest meets the tundra, one of the primary threats Semipalmated Plover are facing in Churchill during the breeding season could be habitat loss related to shrubification. Shrubification has been documented in Churchill (Robinson et al. 2021), and while no specific causality has been established having an impact on this species, shrubs encroaching on the barren habitats used by breeding Semipalmated Plover will reduce the amount of available nesting habitat, and it is likely that this is already happening. These impacts will be most obvious at the inland sites closer to the treeline where the effects of shrubification are greater due to higher vegetative growth, as opposed to the coastal and tundra sites where there is generally less vegetation. In addition, positive-feedback loops associated with shrubification will likely make these effects more pronounced in the future (Zhang et al. 2013), which could cause rapid losses of appropriate nesting habitat for this species in the Hudson Bay lowlands.

Natural habitat alteration caused by isostatic rebound is another factor likely to impact habitat use by Semipalmated Plover in the Hudson Bay lowlands, although the effects are difficult to predict as there is some potential for both positive and negative impacts of this process due to the creation of additional intertidal marsh habitat (Martini et al. 2019), and the reduction of inland habitats associated with shrubification (Ballantyne and Nol 2015). During the last glacial period, Earth's crust was depressed by the weight of glaciers. Isostatic rebound is the subsequent relief of the crust after glaciers melt, with the Churchill region experiencing relatively high rebound rates of 0.9 m/century. The effects of isostatic rebound have the potential to create additional intertidal marshes and beach ridges used by nesting Semipalmated Plover, although it is difficult to predict if this effect will offset the habitat lost to sea level rise as climate change progresses (Martini et al. 2019). Additionally, any positive effects of this process in some areas will be further offset by isostatic rebound accelerating rates of shrubification at inland sites (Ballantyne and Nol 2015). Thus, there is a need for habitat modelling that investigates the impact of both factors on coastal wetlands in the sub-Arctic, and the implications of this for nesting shorebirds.

In addition to the effects of isostatic rebound and sea level rise, rising Canada Goose (*Branta canadensis*) and Snow Goose (*Anser caerulescens*) populations are also likely to have an impact on breeding Semipalmated Plover in the sub-Arctic, especially in the coastal marshes discussed above. In general, plovers choose nest sites that have little or no vegetation, however they will also tolerate low-lying vegetation such as *Dryas integrifolia* at sites with dry substrate and *Puccinelia phryganodes* at wetter coastal intertidal marshes. One such coastal marsh site in Churchill called Bird Cove (BC in Table 3.5) has experienced the well-documented issue of overgrazing by migratory and breeding geese (Kotanen and Abraham 2013), resulting in much of the habitat reaching a degraded state which may negatively impact the likelihood of plovers occupying these sites during the breeding season.

I also documented two instances of nest failure due to the presence of breeding geese in this habitat. This failure was caused by the nests being trampled by large numbers of Canada Goose adults and chicks moving through the nest site repeatedly. The two nests were discovered with crushed eggs, and trail cameras captured hundreds of photographs of the geese moving through the site (Figure 4.1), which eventually led to the nest failure. As well, a third nest was discovered at the Western Estuary site with crushed eggs that we suspect were also the result of Canada Goose trampling. The Bird Cove site experienced a decline in the average number of nest pairs through the 31-year study period. Thus, because of the negative effects of high goose abundance on both habitat quality and nest success, it is likely that the presence of geese at this and other sites could have contributed to the decline at this specific site and in the entire Churchill region.

Figure 4.1. Trail camera image captured at a Semipalmated Plover nest site with the approximate nest location circled in red at Bird Cove (BC in Table 3.5) near Churchill, MB with one Semipalmated Plover and 15 Canada Goose in frame. The nest was eventually trampled by the large number of Canada Goose nesting in the area.

A final potential contributor to the decline of Semipalmated Plover in Churchill is the disturbance from multiple sources across the region related to human activity. First, Churchill experiences a large amount of tourism throughout the summer months, some of which takes large vehicles called "tundra buggies" directly through areas that often have a high number of Semipalmated Plover nests. These vehicles, in addition to smaller vehicles such as trucks and ATVs, have been documented driving very close to nests (Figure 4.2) and could easily crush nests or chicks without being noticed by operators. Next, one site in the region (MP in Figure 2.1 and Table 3.5; “Miss Piggy”) which has experienced significant declines in the number of nesting pairs between the first and second halves of the study period (Table 3.5) is used for gravel mining and has had increasing levels of disturbance in recent years. In fact, in 2023 the Town of Churchill began extensive construction projects to repair the Churchill River weir and the rail line to Churchill using gravel from this site and thus they greatly expanded their efforts here to include blasting of coastal bluffs and crushing large amounts of this rock at the site resulting in much more extreme levels of disturbance to birds in the area (Figure 4.3). The activity at this site seems to be the most likely explanation for the reduction in the number of nests here and has also likely contributed to the region-wide decline in Semipalmated Plover, and with the expansion of construction in the region these negative effects could become more severe.

Figure 4.2. A trail camera photograph of a “tundra buggy” driving through a Semipalmated Plover nest site near Churchill, MB with the approximate nest location circled in red.

Figure 4.3. Photograph of the disturbance at the Miss Piggy (MP) site near Churchill, MB that has recently experienced a high level of disturbance from gravel production.

Vital rate estimates

I successfully obtained vital rate estimates of adult and juvenile apparent survival, fecundity, and immigration for each of the 31 years (1992-2022) that the Churchill Semipalmated Plover population was studied and obtained future estimates for the next twenty years (2023-2042). I also successfully obtained an estimate of nest survival rate for the entire study period, despite missing 12 years of daily nest survival data (e.g., records of visits and outcomes at each visit).

The average adult apparent survival rate (ϕ_{ad} = 0.739) that I obtained was higher than another Semipalmated Plover adult survival estimate of 0.649 ± 0.047 SE from Akimiski Island, Nunavut (Lishman et al. 2010). This estimate is also slightly greater than a previously calculated adult apparent survival estimate (ϕ_{ad} = 0.71 ± 0.036 SE) that used the first seven years of data for the Churchill Semipalmated Plover local population (Badzinski 2000). My estimate likely represents the best estimate of adult survival for this species as it incorporates significantly more data (n = 1359) than any previous estimate.

This estimate of adult apparent survival (ϕ = 0.739) is relatively high among North American *Charadrius* and the closely related *Anarhynchus* (formerly *Charadrius*) plover species. Estimates of adult apparent survival among other plovers are: ϕ = 0.77 in Wilson's Plover (*A. wilsonia*) (DeRose-Wilson et al. 2013), ϕ = 0.725–0.742 in female and male Piping Plover (*C. melodus*) (Saunders et al. 2014), although range wide estimates vary between ϕ = 0.56–0.81 depending on subspecies (Roche et al. 2010), ϕ = 0.68 in Mountain Plover (*A. montanus*) (Dinsmore et al. 2010), and ϕ = 0.51–0.61 in female and male Snowy Plover (*A. nivosus*) (Mullin et al. 2010)). The only other species of plover in North America, excluding *Pluvialis spp.*, Killdeer (*C. vociferus*), has no available estimate. It has been speculated that interspecific variability in apparent survival rates in other *Charadrius* plovers could in part be related to differences in body size (Sandercock et al. 2005), with smaller species having lower survival rates. There is perhaps some evidence for this notion when comparing these species, with Snowy Plover being the smallest and having the lowest survival rate, and Wilson's Plover being the second largest with the highest survival rate (excluding one population of Piping Plover in the Great Plains with a range between 0.69-0.81 (Roche et al. 2010)). However, Mountain Plover are the largest species with the second lowest survival rate, and thus there are likely other confounding factors such as variability in encounter probability and site fidelity (Sandercock et al. 2005) that make this pattern less clear.

Juvenile apparent survival in my base model (ϕ_{juv} = 0.073) was slightly higher on average than what had previously been reported (ϕ_{juv} = 0.047, 95% CI: 0.030–0.075) for this population of Semipalmated Plovers, although not outside of the confidence interval (Nol et al. 2010). For the period of study in Badzinski (2000), juvenile apparent survival was not modelled as there were only 5 resights of individuals captured as chicks during this period and thus the sample size was too small for a reliable estimate. Like the differences between current and past estimates of adult apparent survival, this slightly higher juvenile apparent survival rate is likely a reflection of the larger sample size of marked individuals (i.e, n = 2061 vs n = 1271) than what was used in Nol et al. (2010), and thus represents the best estimate to date for this species.

This estimate of juvenile apparent survival is the lowest reported for any North American *Charadrius* or *Anarhynchus* plover. Estimates reported for other plovers are: ϕ = 0.46–0.49 in Mountain Plover (Dinsmore et al. 2010), ϕ = 0.40 ± 0.06 in Snowy Plover (Mullin et al. 2010), and ϕ = 0.284 ± 0.019 SE in Piping Plover (Saunders et al. 2014), with no estimates available for Wilson's Plover or Killdeer. This extremely low juvenile apparent survival rate is likely related to differences in both study limitations and interspecific differences in ecology. First, because juveniles in this study were usually captured one to three days after hatch, the survival rate then also incorporates the fledging rate of these individuals and thus will result in a lower rate and is not directly comparable with traditional analyses. Next, surveying for Semipalmated Plovers dispersing short distances relative to other species is comparatively very difficult in the sub-Arctic due to the rough terrain and inaccessibility as there are no maintained roads approximately 25 km outside of Churchill. In comparison, the other species mentioned are all studied in the

United States in relatively urbanized areas which makes surveying a larger area possible and thus increases the likelihood of resighting dispersing juveniles. As well, having a higher number of observers, many of which could just be local birders, increases this likelihood even more. In species such as Piping Plover, extremely long natal dispersal distances of over 1000 km have been recorded multiple times (Brown et al. 2022), thus resighting juvenile dispersers can be near-impossible in plovers without a very large study area. Thus, because apparent survival incorporates both true survival and permanent emigration, and plovers are known to disperse very far from natal sites (Brown et al. 2022), this estimate of apparent survival does not fully reflect the true survival rate of juvenile Semipalmated Plover.

Juvenile apparent survival is much lower in Semipalmated Plover than what is observed in closely related plover species, but it is not atypical to what is usually seen in other Arctic nesting shorebirds, although estimates are scarcely available. For example, in a local population of Semipalmated Sandpiper (*Calidris pusilla*) studied approximately 40 km from Churchill at La Perouse Bay, Manitoba, juvenile apparent survival was $\phi = 0.09$, 95% CI = 0.06-0.16 (Sandercock and Gratto-Trevor 1997). As well, a study examining return rates of 10 shorebird species in Barrow, Alaska banded 2979 chicks between 2003–2012 and recorded only one individual returning to breed in their study plots, and recorded an additional seven resights of three species without confirmed breeding (Saalfeld and Lanctot 2015). Considering 65 of 2061 banded Semipalmated Plover chicks returned to Churchill, this return rate is remarkably high when compared with other Arctic breeding shorebirds. Low rates of return, and thus low juvenile apparent survival, in many Arctic shorebirds is likely a product of the evolutionary benefits of dispersing at high latitudes (Saalfeld and Lanctot 2015). Saalfield and Lanctot (2015) discuss several studies that document higher rates of return and nesting densities at more southern latitudes in other shorebirds and suggested that this pattern is related to higher resource predictability in the south. My findings further support the idea that unpredictable resources in the North result in lower site fidelity, especially in juveniles. Another potential explanation for this dispersal in Arctic shorebirds could be that habitat may be more limited at southern latitudes than in the north, causing a greater cost of dispersal in southern birds. Conversely, although resources are unpredictable in the Arctic, there could still be a lower cost of dispersal because, anecdotally, habitat in the Arctic does not appear to be limited.

My estimate of average fecundity ($f = 2.02$) for the study period represents the first estimate of this vital rate in Semipalmated Plover. Fecundity is generally difficult to estimate in most shorebirds as the data needed require extensive monitoring of many nests in a population to find the number of young produced per female. Additional difficulty in comparing this estimate to those in the literature is added by researchers estimating this rate at differing stages of the reproductive process. For example, estimates of fecundity exist for Piping Plover, Snowy Plover, and Mountain Plover, but these were estimated as the number of fledglings per female (Mullin et al. 2010, van der Burg and Tyre 2011, Saunders et al. 2018). However, my estimate was made as the number of chicks per female (i.e., excluding the fledge rate), due to the difficulty in tracking fledging rate in this study, and instead fledging is included in the model through the juvenile survival rate as this is calculated for chicks captured shortly after hatch (generally 1–3 days old), many of which do not fledge.

Because this fecundity rate is >1, this means on average a female in this population was able to successfully replace herself and in many species, especially those with shorter lifespans, this would result in a strong contribution to population growth (Sæther and Bakke 2000). Semipalmated Plover are a relatively long-lived species and thus a weaker contribution to population growth would be expected. As well, because of high juvenile dispersal a weak contribution of fecundity despite a relatively high rate would be expected. Finally, because many of the individuals included in this fecundity estimate likely did not fledge, the true reproductive output is certainly lower and thus would yield a weaker contribution to population growth rate. Of the four vital rates estimated, fecundity had the second lowest likelihood of a positive correlation with population growth rate which supports this notion of a weak contribution of fecundity to population growth.

My estimate of the average immigration rate ($\omega = 0.219$), the number of immigrants per female, represents the first estimate of this vital rate in Semipalmated Plover. Immigration is notoriously difficult to estimate in population studies as explicit data on this rate are rarely available. It was only possible to estimate here because IPMs account for all other vital rates in one integrated analysis. Although immigration has not previously been estimated for this species, Badzinski (2000) speculated that the immigration rate of this species in Churchill was likely to contribute significantly to population dynamics as their stage-structured matrix models (Hitchcock and Gratto-Trevor 1997) indicated that the population should be in decline (i.e., $\lambda < 1$), however they observed no decline during their fieldwork. Additionally, in some years many of the breeding adults observed in the population were unbanded and were thus suspected to be immigrants. My findings confirm this suspicion as immigration was the vital rate most highly correlated with population growth. This finding also supports the idea that there is high juvenile dispersal causing low juvenile apparent survival in this population, as many of the immigrants to the Churchill study area are likely to be young birds dispersing from other breeding areas in the Arctic. While it has been shown that immigration estimates calculated using IPMs are often biased (Paquet et al. 2021), this issue was also found to be less severe in populations where there was high interannual variation in immigration rates. Immigration estimates in this study were highly variable, and the observed number of suspected immigrants was also quite variable between years. Thus, the degree of bias in my immigration values may not be as severe as in some of the case studies reviewed by Paquet et al. (2021).

Few other estimates of immigration for plover species exist in North America. In Piping Plover, this rate was estimated as 0.36 to 0.55 immigrants per resident (Robinson et al. 2020), much higher than my estimate. Another study of Piping Plovers in the Great Lakes found an expected number of 2.65 immigrants to the population each year, with a high of 7.89 immigrants in one year (Saunders et al. 2018) in a population similar in size (roughly 20–80 pairs) to the Churchill Semipalmated Plover population (roughly 20–60 pairs). My average estimate for the number of immigrants across all years was 7.21 immigrants, with a range between 2.06 and 27.77, illustrating the much stronger relationship between immigration and population growth seen in this population in comparison to Piping Plovers in the Great Lakes. Much higher contributions of immigration to population growth have been seen in Snowy Plover compared to those in both Semipalmated and Piping Plover. A study in Northern California found that 63 ± 5% of the entire population was comprised of immigrants over a period of 12 years (Colwell et al. 2017). Colwell et al. (2017) classified the population as a demographic sink, a population where mortality does not exceed reproductive rates and thus must be supplemented by immigrants to sustain itself. Given the low contribution of fecundity and high contribution of immigration to population growth seen in my study, this population could also potentially be considered a sink. However, as previously discussed, this pattern of high immigration rates likely caused by high juvenile dispersal is seen in many other species of Arctic shorebirds, and thus this may be a natural phenomenon exhibited by most shorebird populations breeding in the north.

Future population predictions

I obtained future population growth rate estimates under three different climate change scenarios for the next 20 years using a coupled IPM-PVA approach. Overall, future population size estimates in each scenario were similar to what was seen throughout the study, albeit with a gradual increase over time of roughly 2.5% per year over the 20 simulated years. This finding was surprising considering the many negative effects of climate change predicted for this and other shorebird species, and the slight decline observed in this population in the second half of the study period. However, because future spring temperature estimates were used to inform this PVA, and a positive effect of spring temperature on juvenile apparent survival was found, this increase over time was expected.

Interestingly, of the PVA models, the one with the best performance was for the intermediate emissions scenario, SSP 4-3.4, and this scenario also predicted the greatest increase in future population size despite a lower temperature in year 50 than the most severe scenario, SSP 5-8.5. However, there was little difference in the predictions between the three scenarios, with quasi-extinction probabilities varying only between roughly 0.3–0.4% in the final year of simulations. This low likelihood of quasi-extinction suggests there is some resilience of this species to the effects of climate change, despite recent declines in their range-wide population (Smith et al. 2023). A similar analysis for Piping Plovers investigating the effects of various predator control scenarios by Saunders et al. (2018) found varying quasi-extinction thresholds between roughly 2–12%, significantly higher than what I found for Semipalmated Plover. This difference can largely be explained by two factors. First, because of the role immigration plays in Semipalmated Plover population dynamics, reaching a quasi-extinction threshold seems less likely as deaths in the population could be offset by a relatively high rate of immigration assuming other populations within dispersal distances are healthy. As well, my study investigated the effects of a covariate that had a positive effect on survival, while Saunders et al. (2018) investigated the effect of a covariate for Merlin (*Falco columbarius*) abundance which negatively impacted survival. Thus, if Merlin abundance was not controlled in future scenarios a greater likelihood of reaching the quasi-extinction threshold was expected.

Effect of spring temperature

The effect of temperature and other climatic variables have been considered for some time in this species, however up until this study only a moderate effect on nest success (Badzinski 2000) and chick rearing behaviour (Blanken and Nol 1998) had been found. This lack of evidence for effects of climate on processes contributing to Semipalmated Plover population dynamics does not necessarily mean that no effects exist though, as it has been suggested that these trends often only become apparent over a longer timescale (Sandercock and Gratto-Trevor 1997). Sandercock and Gratto-Trevor (1997) investigated impacts of weather on Semipalmated Sandpiper survival and found no effect, however their study took place over only 8 years. Similarly, Badzinski (2000) was not able to find an effect of temperature on survival but only used 7 years of data. Conversely, my study used 31 years of data and was able to detect an effect of spring minimum temperature, supporting the idea that long-term studies are often required to detect effects of climatic variables on population dynamics.

Underlying mechanisms of climatic variables influencing population dynamics in shorebirds have been suggested such as impacts on prey availability (Pearce-Higgins et al. 2005), shifting predator communities (Kubelka et al. 2018), changes in breeding phenology (Abernathy et al. 2023), and changes in clutch sizes (Nol et al. 1997). Effects of these changes are difficult to predict though and are likely specific to each study system. For example, a similar positive effect of minimum temperature was found on Snowy Plover clutch size and nest fate (Zhao et al. 2021). These authors suggested that the mechanism behind this pattern (i.e., warmer overnight temperatures leading to more successful incubation) could also be offset by the effects of greater daily maximum temperatures leading to drought which could dry up wetlands this species relies on for foraging. All the above changes are likely to impact breeding Semipalmated Plover, and thus interpreting any positive effect of climate change on this species must be done with caution. For example, while prey availability may increase with warming temperatures, the timing of this availability may offset any positive effect as warmer springs may lead to early arrival and clutch initiation, which could cause a phenological mismatch (Saalfeld et al. 2019) meaning chicks may hatch before there is enough prey for them to survive to fledge. Despite this asynchrony being documented in Churchill, there is currently no evidence that this is negatively impacting Semipalmated Plover chick growth rates (Corkery et al. 2019). In fact, increased chick growth rates at warmer temperatures despite below average below average resource availability have been seen in Dunlin (*Calidris alpina*) in Churchill (McKinnon et al. 2013). However, as the effects of climate change become more severe this positive effect could reverse if the asynchrony between hatch and peak resource availability timing becomes more pronounced, or if there is some threshold where warmer temperatures begin to negatively impact chick development. Additionally, the effects of climate change are influencing predator communities in the region (Verstege et al. 2023), the impacts of which could be unpredictable for breeding shorebirds.

The exact mechanism driving the increased juvenile apparent survival in Semipalmated Plover is unclear and may also be related to untested processes. This pattern becomes more unclear when considering that apparent survival also involves the permanent emigration of juveniles from the study area, and thus this increased vital rate could simply be the result of more birds returning to their natal sites to breed, and not an impact on true survival. Perhaps this is because young birds only return to the natal sites to breed under ideal conditions in seasons with higher prey availability in the spring? Another potential factor involved is the ease of migration in years with warmer spring temperatures leading to inexperienced birds migrating further than usual (i.e., stronger southerly winds leading to warmer spring temperatures could make migration easier for juveniles). Finally, it is possible that juveniles do return more often than we know in the region, however due to possible habitat limitation in early spring (i.e., many sites being covered in snow, or too wet from snowmelt, upon arrival in spring) these birds may decide to disperse rather than attempt to compete with more experienced individuals that claim the limited habitats early on. Thus, more study is required to fully understand the mechanisms and impacts involved with warming temperature influencing Semipalmated Plover population dynamics in the sub-Arctic.

Changing avian populations in Churchill

The effect of climate change on Semipalmated Plover in Churchill, Manitoba, and the potential decline of this species in the region is especially troubling as this is not the first species to experience declines near Churchill. For example, Semipalmated Sandpiper were once the most abundant nesting sandpiper in the area, but experienced drastic declines beginning in the 1960s leading to their extirpation from the Churchill study area (Jehl 2007). Similarly, Lapland Longspur (*Calcarius lapponicus*) once commonly nested throughout the region but experienced significant declines throughout the 20th century (Boal and Andersen 2005) and are now likely extirpated from much of the area between Churchill and Cape Churchill. Additionally, a rarer species, Smith's Longspur (*Calcarius pictus*) also historically nested sparsely throughout the region and now individuals are observed near the town less than annually. Whimbrel (*Numenius* *phaeopus*) still nest in the region but have also experienced troubling declines (Jehl and Lin 2001) possibly related to reduced fecundity (Ballantyne and Nol 2011). Declines in the region are clearly not isolated to one species and thus the beginning of a decline for Semipalmated Plover in the region is not to be taken lightly. Additional study on this and the other species that occupy the region are thus imperative, because if this pattern continues changes in the avifauna communities of Churchill may be irreversible.

Study limitations

The main challenge encountered in this study was the interpretability of some results due to varying data collection effort over time. For the most part nest searching effort remained consistent over time, but there were some differences that can make the population estimates less precise. This study officially began in 1992 and was not specifically designed as a large-scale population monitoring effort. Instead, depending on the project of interest by various students involved, some years focused on a larger search area and some years a smaller area. For example, if a student was interested in capturing a high number of birds for a migration tracking study, they would then expand the search area such that they could find enough nests to have a high sample size of captured adults. Conversely, if a student was more interested in behavioural analysis, they may have spent a greater amount of time observing fewer nests. These differences do not mean that population estimates are entirely untrustworthy though, instead they mean that interpretation of these results must be done with more consideration of the varying search effort summarized in Table 3.5. Thus, while changes in population estimates over time do reflect true changes in the population size over time, there is also some (unknown) degree of change related to search effort.

Another limitation to consider is that the return rates of individuals captured as chicks are likely underinflated as there were two issues encountered that made the detection of these individuals imperfect. First, because these birds often did not return to the breeding area for multiple years after they were first encountered, the amount of wear on their metal bands (likely due to saltwater exposure) made it such that there were some individuals whose exact identification was impossible. This was either because the band was too worn to read (seen only 1–2 times per year), or in one rare case the band fell off, resulting in individuals considered "dead" in the models even though they were still contributing to the population. Second, between 1992–2019 chicks were only given brood-specific (i.e., not individually identifiable) band combinations, and thus these individuals had to be recaptured to be identified. Generally, this was done with ease, however there were rare cases where these individuals refused to accept traps placed on nests and thus were unable to be recaptured and identified. Therefore, the true juvenile apparent survival rates should be assumed to be slightly higher than what I found in my analysis.

<u>Future directions</u>

First, a large advantage to using IPMs is that once the model code has become established, updating the models as future data are collected is trivial as this only involves simply updating data files and rerunning analyses. Thus, my study has accomplished an easy way to continue monitoring and analyzing changes in this population over time. Also, as new data are collected, the established model code can be updated to investigate the effects of covariates not considered in my study. Some suggestions for future study investigating potential drivers of population change could be the effects of changing goose abundance, shrubification, changing predator communities (namely foxes, Common Raven (*Corvus corax*), and Merlin), other climatic variables not considered in my study, and human disturbance in terms of industrial development, gravel extraction, residential development, and tourism. Finally, I would like to attempt to model the relative levels of effort between years to obtain less biased population estimates, which would require creating a method for quantifying the differences in effort between years.

Chapter 5: Summary and Conclusions

My research is the first to use integrated population modelling for Semipalmated Plover and provides the best estimates to date for all vital rates, including fecundity and immigration. These two vital rates had previously not been estimated in this species and are rarely estimated for any species of Arctic nesting shorebird (Pakanen et al. 2016, Weiser et al. 2018). I also provide updated estimates of overall population trends in the region which had not been analyzed in the past 20 years. I obtained estimates of population size and growth rate between 1992-2022 and found that throughout the study period, the population remained generally stable with a high degree of interannual variability. Posterior average estimates of population growth rate (λ) ranged between 0.58–2.13, with an average of 1.02 across the 31-year period. Additionally, I found that there was an average decline in population growth in the second half of the study period ($\lambda = 0.97$), likely due to site specific declines in habitats that may be experiencing some level of degradation.

I obtained estimates of yearly vital rates (adult apparent survival, juvenile apparent survival, fecundity, and immigration) as well as an overall average for each, and calculated correlation coefficients between all vital rates and the population growth rate. I found that population growth was most highly correlated with immigration and adult apparent survival, and that there was virtually no correlation between population growth rate and fecundity or juvenile apparent survival. Also, although juvenile apparent survival was very low throughout the study period and thus had little correlation with population growth, I found a positive effect of spring minimum temperature on this vital rate. This finding suggests that Semipalmated Plover possess some level of resilience to the effects of climate change. While there are many interacting and complex factors at play when considering the impacts of climate change more study needs to be done on the implications of changes in the sub-Arctic to develop a better understanding of how this species will respond.

The effect of spring temperature on juvenile apparent survival was used in conjunction with future local temperature estimates from global climate models to predict population sizes 20 years into the future in Churchill. Through this I found that there was a low, albeit non-zero, chance of the population going below a quasi-extinction threshold of 10 nesting pairs, and I found that there is a higher probability of the population increasing over time when considering the effects of future temperature, again pointing to the resilience of this species to some effects of climate change. This resilience is underscored when considering the other species that have severely declined or even disappeared from the Churchill region in recent history such as Whimbrel (Ballantyne and Nol 2015) and Semipalmated Sandpiper (Jehl 2007). My research has laid the groundwork for future studies that could continue to use population monitoring data for this species in Churchill and use the now established modelling framework to analyze these data with ease and investigate the effects of other covariates on population dynamics. This framework will hopefully be used to explore the implications of climate change, shifting predator abundances, and the development of northern communities on Semipalmated Plover population dynamics.

Appendix

Appendix 1. JAGS Code for "Base model" integrated population model. Code adapted from Kery and Schaub (2011) and Saunders et al. (2018).

```
#----------------------------------------
# 1. Define the priors for the parameters
#----------------------------------------
# Initial population sizes
n1 ~ dnorm(100, 0.0001)I(0,)          # 1-year old individuals
nadSurv ~ dnorm(100, 0.0001)I(0,)     # Adults >= 2 years
nadimm ~ dnorm(100, 0.0001)I(0,)      # Immigrants
N1[1] <- round(n1)
NadSurv[1] <- round(nadSurv)
Nadimm[1] <- round(nadimm)
R[29] ~ dunif(0,70)
# Mean demographic parameters (on appropriate scale)
l.mphij ~ dnorm(0, 0.0001)I(-10,10)
l.mphia ~ dnorm(0, 0.0001)I(-10,10)
l.mfec ~ dnorm(0, 0.0001)I(-10,10)
l.mim ~ dnorm(0, 0.0001)I(-10,10)
l.p ~ dnorm(0, 0.0001)I(-10,10)
beta ~ dnorm(0, 0.0001)
# Precision of standard deviations of temporal variability
sig.phij ~ dunif(0, 10)
tau.phij <- pow(sig.phij, -2)
sig.phia ~ dunif(0, 10)
tau.phia <- pow(sig.phia, -2)
sig.fec ~ dunif(0, 10)
tau.fec <- pow(sig.fec, -2)
```

```
sig.im ~ dunif(0, 50)
tau.im <- pow(sig.im, -2)
# Distribution of error terms (Bounded to help with convergence)
for (t in 1:(nyears-1)){
  epsilon.phij[t] ~ dnorm(0, tau.phij)T(-5,5)
  epsilon.phia[t] ~ dnorm(0, tau.phia)T(-5,5)
  epsilon.fec[t] ~ dnorm(0, tau.fec)T(-5,5)
  epsilon.im[t] ~ dnorm(0, tau.im)T(-5,5)}
#-------------------------
# 2. Constrain parameters
#-------------------------
for (t in 1:(nyears-1)){
  logit(phij[t]) <- l.mphij + epsilon.phij[t]  + beta*temp[t] # Juv. apparent survival
  logit(phia[t]) <- l.mphia + epsilon.phia[t]                 # Adult apparent survival
  log(f[t]) <- l.mfec + epsilon.fec[t]                        # Productivity
  log(omega[t]) <- l.mim + epsilon.im[t]                      # Immigration
  logit(p[t]) <- l.p                                          # Recapture probability}
#-----------------------
# 3. Derived parameters
#-----------------------
mphij <- exp(l.mphij)/(1+exp(l.mphij))    # Mean juvenile survival probability
mphia <- exp(l.mphia)/(1+exp(l.mphia))  # Mean adult survival probability
mfec <- exp(l.mfec)                     # Mean productivity
mim <- exp(l.mim)                       # Mean immigration rate

# Population growth rate
for (t in 1:(nyears-1)){
  lambda[t] <- Ntot[t+1] / Ntot[t]
  logla[t] <- log(lambda[t])}
mlam <- exp((1/(nyears-1))*sum(logla[1:(nyears-1)]))   # Geometric mean
```

```
#-----------------------------------------
# 4. The likelihoods of the single data sets
#-----------------------------------------
# 4.1. Likelihood for population population count data (state-space model)
  # 4.1.1 System process
  for (t in 2:nyears){
    mean1[t] <- 0.5 * f[t-1] * phij[t-1] * Ntot[t-1]
    N1[t] ~ dpois(mean1[t])
    NadSurv[t] ~ dpois(phia[t-1]*Ntot[t-1])
    mpo[t] <- Ntot[t-1] * omega[t-1]
    Nadimm[t] ~ dpois(mpo[t])}
  # 4.1.2 Observation process
  for (t in 1:nyears){
    Ntot[t] <- NadSurv[t] + Nadimm[t] + N1[t]
    y[t] ~ dpois(Ntot[t])}
# 4.2 Likelihood for capture-recapture data: CJS model (2 age classes)
# Multinomial likelihood
for (t in 1:(nyears-1)){
  marray.j[t,1:nyears] ~ dmulti(pr.j[t,], r.j[t])
  marray.a[t,1:nyears] ~ dmulti(pr.a[t,], r.a[t])}
# m-array cell probabilities for juveniles
for (t in 1:(nyears-1)){
  q[t] <- 1-p[t]
  # Main diagonal
  pr.j[t,t] <- phij[t]*(p[t]*dummy[t])
  # Above main diagonal
  for (j in (t+1):(nyears-1)){
    pr.j[t,j] <- phij[t]*prod(phia[(t+1):j])*prod(q[t:(j-1)])*(p[j]*dummy[t])} #j (year)
  # Below main diagonal
  for (j in 1:(t-1)){
```

```
    pr.j[t,j] <- 0} #j
  # Last column
  pr.j[t,nyears] <- 1-sum(pr.j[t,1:(nyears-1)])} #t
# m-array cell probabilities for adults
for (t in 1:(nyears-1)){
  # Main diagonal
  pr.a[t,t] <- phia[t]*(p[t]*dummy[t])
  # above main diagonal
  for (j in (t+1):(nyears-1)){
    pr.a[t,j] <- prod(phia[t:j])*prod(q[t:(j-1)])*(p[j]*dummy[t])} #j
  # Below main diagonal
  for (j in 1:(t-1)){
    pr.a[t,j] <- 0} #j
  # Last column
  pr.a[t,nyears] <- 1-sum(pr.a[t,1:(nyears-1)])} #t
# 4.3. Likelihood for productivity data: Poisson regression
for (t in 1:(nyears-1)){
  J[t] ~ dpois(rho[t])
  rho[t] <- R[t] * f[t]}
```

Appendix 2. Code for "Nest survival" iteration of the IPM. Code adapted from Kery and Schaub (2011) and Saunders et al. (2018).

```
#---------------------------------------
# 1. Define the priors for the parameters
#---------------------------------------
# Initial population sizes
n1 ~ dnorm(100, 0.0001)I(0,)          # 1-year old individuals
nadSurv ~ dnorm(100, 0.0001)I(0,)      # Adults >= 2 years
nadimm ~ dnorm(100, 0.0001)I(0,50)       # Immigrants
N1[1] <- round(n1)
NadSurv[1] <- round(nadSurv)
Nadimm[1] <- round(nadimm)
beta ~ dnorm(0, 0.0001)
# Mean demographic parameters (on appropriate scale)
l.mphij ~ dnorm(0, 0.0001)I(-10,10)
l.mphia ~ dnorm(0, 0.0001)I(-10,10)
l.mim ~ dnorm(0, 0.0001)I(-10,10)
l.p ~ dnorm(0, 0.0001)I(-10,10)
l.NS ~ dnorm(0, 0.0001)I(-5,5)
# Precision of standard deviations of temporal variability
sig.phij ~ dunif(0, 10)
tau.phij <- pow(sig.phij, -2)
sig.phia ~ dunif(0, 10)
tau.phia <- pow(sig.phia, -2)
sig.im ~ dunif(0, 10)
tau.im <- pow(sig.im, -2)
sig.ds ~ dunif(0, 10)
tau.ds <-pow(sig.ds, -2)
sig.NS ~ dunif(0,5)
tau.NS <-pow(sig.NS, -2)
```

```
# Distribution of error terms
for (t in 1:(nyears-1)){
  epsilon.phij[t] ~ dnorm(0, tau.phij)T(-5,5)
  epsilon.phia[t] ~ dnorm(0, tau.phia)T(-5,5)
  epsilon.im[t] ~ dnorm(0, tau.im)T(-5,5)
  epsilon.NS[t] ~ dnorm(0, tau.NS)T(-5,5)}
#------------------------
# 2. Constrain parameters
#------------------------
for (t in 1:(nyears-1)){
  logit(phij[t]) <- l.mphij + epsilon.phij[t] + beta * temp[t] # Juv. apparent survival
  logit(phia[t]) <- l.mphia + epsilon.phia[t]  # Adult apparent survival
  log(omega[t]) <- l.mim + epsilon.im[t]      # Immigration
  logit(p[t]) <- l.p                           # Recapture probability
  logit(mu.ds[t]) <- l.NS + epsilon.NS[t]      # Mean daily nest survival }
#----------------------
# 3. Derived parameters
#----------------------
mphij <- exp(l.mphij)/(1+exp(l.mphij))   # Mean juvenile survival probability
mphia <- exp(l.mphia)/(1+exp(l.mphia))   # Mean adult survival probability
mfec <- exp(l.NS)/(1+exp(l.NS))          # Mean nest success probability
mim <- exp(l.mim)                        # Mean immigration rate
# Population growth rate
for (t in 1:(nyears-1)){
  lambda[t] <- Ntot[t+1] / Ntot[t]
  logla[t] <- log(lambda[t])}
mlam <- exp((1/(nyears-1))*sum(logla[1:(nyears-1)]))   # Geometric mean
#------------------------------------------
# 4. The likelihoods of the single data sets
#------------------------------------------
```

```
# 4.1. Likelihood for population population count data (state-space model)
  # 4.1.1 System process
  for (t in 2:nyears){
    mean1[t] <- 0.5 * rho[t-1] * phij[t-1] * Ntot[t-1]
    N1[t] ~ dpois(mean1[t])
    NadSurv[t] ~ dpois(phia[t-1]*Ntot[t-1])
    mpo[t] <- Ntot[t-1] * omega[t-1]
    Nadimm[t] ~ dpois(omega[t-1])}
  # 4.1.2 Observation process
  for (t in 1:nyears){
    Ntot[t] <- NadSurv[t] + Nadimm[t] + N1[t]
    y[t] ~ dpois(Ntot[t])}
# 4.2 Likelihood for capture-recapture data: CJS model (2 age classes)
# Multinomial likelihood
for (t in 1:(nyears-1)){
  marray.j[t,1:nyears] ~ dmulti(pr.j[t,], r.j[t])
  marray.a[t,1:nyears] ~ dmulti(pr.a[t,], r.a[t])}
# m-array cell probabilities for juveniles
for (t in 1:(nyears-1)){
  q[t] <- 1-p[t]
  # Main diagonal
  pr.j[t,t] <- phij[t]*p[t]*dummy[t]
  # Above main diagonal
  for (j in (t+1):(nyears-1)){
    pr.j[t,j] <- phij[t]*prod(phia[(t+1):j])*prod(q[t:(j-1)])*p[j]*dummy[t]} #j (year)
  # Below main diagonal
  for (j in 1:(t-1)){
    pr.j[t,j] <- 0 } #j
  # Last column
  pr.j[t,nyears] <- 1-sum(pr.j[t,1:(nyears-1)]) } #t
```

```
# m-array cell probabilities for adults
for (t in 1:(nyears-1)){
  # Main diagonal
  pr.a[t,t] <- phia[t]*p[t]*dummy[t]
  # above main diagonal
  for (j in (t+1):(nyears-1)){
    pr.a[t,j] <- prod(phia[t:j])*prod(q[t:(j-1)])*p[j]*dummy[t]} #j
  # Below main diagonal
  for (j in 1:(t-1)){
    pr.a[t,j] <- 0 } #j
  # Last column
  pr.a[t,nyears] <- 1-sum(pr.a[t,1:(nyears-1)]) } #t
# 4.3. Likelihood for productivity data: Mayfield model
for (t in 1:(nyears-1)){
  J[t] ~ dpois(rho[t])
  rho[t] <- y[t] * 2 * NS[t]
  NS[t] <- mu.ds[t]^30
  ds.o[t] ~ dnorm(mu.ds[t], tau.ds)}
```

Appendix 3. JAGS Code for the “PVA” iterations of the IPMs. Code adapted from Kery and Schaub (2011) and Saunders et al. (2018). Differences in the PVA model outputs are due to differences in temperature datasets.

```
#---------------------------------------
# 1. Define the priors for the parameters
#---------------------------------------
# Initial population sizes
n1 ~ dnorm(100, 0.0001)I(0,)          # 1-year old individuals
nadSurv ~ dnorm(100, 0.0001)I(0,)      # Adults >= 2 years
nadimm ~ dnorm(100, 0.0001)I(0,50)      # Immigrants
N1[1] <- round(n1)
NadSurv[1] <- round(nadSurv)
Nadimm[1] <- round(nadimm)
R[29] ~ dunif(0,70)
Ntot[1] <- N1[1] + NadSurv[1] + Nadimm[1]

# Mean demographic parameters (on appropriate scale)
l.mphij ~ dnorm(0, 0.0001)I(-10,10)
l.mphia ~ dnorm(0, 0.0001)I(-10,10)
l.mfec ~ dnorm(0, 0.0001)I(-10,10)
#l.mim ~ dnorm(0, 0.0001)I(-10,10)
l.p ~ dnorm(0, 0.0001)I(-10,10)
beta ~ dnorm(0, 0.0001)
b0.omm ~ dunif(0, 20)        # Expected # of immigrants
#back transformation
log.b0.omm <- log(b0.omm)

# Precision of standard deviations of temporal variability
sig.phij ~ dunif(0, 10)
tau.phij <- pow(sig.phij, -2)
```

```
sig.phia ~ dunif(0, 10)
tau.phia <- pow(sig.phia, -2)
sig.im ~ dunif(0, 10)
tau.im <- pow(sig.im, -2)
sig.fec ~ dunif(0, 10)
tau.fec <- pow(sig.fec, -2)
sig.ds ~ dunif(0, 10)
tau.ds <-pow(sig.ds, -2)

# Distribution of error terms
for (t in 1:(nyears+K)){
  epsilon.phij[t] ~ dnorm(0, tau.phij)T(-5,5)
  epsilon.phia[t] ~ dnorm(0, tau.phia)T(-5,5)
  epsilon.fec[t] ~ dnorm(0, tau.fec)T(-5,5)
  epsilon.im[t] ~ dnorm(0, tau.im)T(-5,5)}

#-------------------------
# 2. Constrain parameters
#-------------------------
for (t in 1:(nyears-1+K)){
  logit(phij[t]) <- l.mphij + epsilon.phij[t] + beta * temp[t] # Juv. apparent survival
  logit(phia[t]) <- l.mphia + epsilon.phia[t]  # Adult apparent survival
  log(f[t]) <- l.mfec + epsilon.fec[t]         # Productivity
  log(omega[t]) <- log.b0.omm + epsilon.im[t]  # Immigration
  logit(p[t]) <- l.p                           # Recapture probability  }

#-----------------------
# 3. Derived parameters
#-----------------------
mphij <- exp(l.mphij)/(1+exp(l.mphij))   # Mean juvenile survival probability
```

```
mphia <- exp(l.mphia)/(1+exp(l.mphia))   # Mean adult survival probability
mfec <- exp(l.mfec)/(1+exp(l.mfec))      # Mean nest success probability
#mim <- exp(l.mim)                       # Mean immigration rate

# Population growth rate
for (t in 1:(nyears-1+K)){
  lambda[t] <- Ntot[t+1] / (Ntot[t] + 0.0001)
  logla[t] <- log(lambda[t])}
mlam <- exp((1/(nyears-1+K))*sum(logla[1:(nyears-1+K)]))   # Geometric mean

#-------------------------------------------
# 4. The likelihoods of the single data sets
#-------------------------------------------
# 4.1. Likelihood for population population count data (state-space model)
  # 4.1.1 System process
  for (t in 2:(nyears+K)){
    Ntot[t] <- NadSurv[t] + Nadimm[t] + N1[t]
    mean1[t] <- 0.5 * f[t-1] * phij[t-1] * Ntot[t-1]
    N1[t] ~ dpois(mean1[t])
    NadSurv[t] ~ dpois(phia[t-1]*Ntot[t-1])
    #mpo[t] <- Ntot[t-1] * omega[t-1]
    Nadimm[t] ~ dpois(omega[t-1]) }

  # 4.1.2 Observation process
  for (t in 1:(nyears)){
    y[t] ~ dpois(Ntot[t]) }

# 4.2 Likelihood for capture-recapture data: CJS model (2 age classes)
# Multinomial likelihood
for (t in 1:(nyears-1)){
```

```
  marray.j[t,1:nyears] ~ dmulti(pr.j[t,], r.j[t])
  marray.a[t,1:nyears] ~ dmulti(pr.a[t,], r.a[t]) }

# m-array cell probabilities for juveniles
for (t in 1:(nyears-1)){
  q[t] <- 1-p[t]
  # Main diagonal
  pr.j[t,t] <- phij[t]*p[t]*dummy[t]
  # Above main diagonal
  for (j in (t+1):(nyears-1)){
    pr.j[t,j] <- phij[t]*prod(phia[(t+1):j])*prod(q[t:(j-1)])*p[j]*dummy[t]} #j (year)
  # Below main diagonal
  for (j in 1:(t-1)){
    pr.j[t,j] <- 0 } #j
  # Last column
  pr.j[t,nyears] <- 1-sum(pr.j[t,1:(nyears-1)]) } #t

# m-array cell probabilities for adults
for (t in 1:(nyears-1)){
  # Main diagonal
  pr.a[t,t] <- phia[t]*p[t]*dummy[t]
  # above main diagonal
  for (j in (t+1):(nyears-1)){
    pr.a[t,j] <- prod(phia[t:j])*prod(q[t:(j-1)])*p[j]*dummy[t] } #j
  # Below main diagonal
  for (j in 1:(t-1)){
    pr.a[t,j] <- 0} #j
  # Last column
  pr.a[t,nyears] <- 1-sum(pr.a[t,1:(nyears-1)])} #t
```

```
# 4.3. Likelihood for productivity data: Mayfield model
for (t in 1:(nyears-1)){
   J[t] ~ dpois(rho[t])
   rho[t] <- R[t]*f[t]}}
```

Appendix 4. Key to study site name abbreviations used in Figure 2.1 and Table 3.5.

Site abbreviation	Full name
WE	Western Estuary
TL	Twin Lakes
GB	Golf Balls
HP	Halfway Point
EP	East Point
EE	East of East Point
FL	The Flats
LL	Landing Lake
OC	Old Coast Road
CNSC	Churchill Northern Studies Centre
HT	Hydro Tower
PR	Palsa Road
MP	Miss Piggy
ER	End of Runway
DB	Dump Beach
MD	Metal Dump Road
IB	Ithaka Bay
AK	Akudlik Marsh
BC	Bird Cove
MISC	Miscellaneous

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