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Modelling the Impact of Climate Change on the Polar Bear Population in Western Hudson Bay

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Applied Mathematics

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Abstract

The aim of this thesis is to model the impact of climate change on polar bear populations. The first model is a discrete matrix model with time-dependent parameters, which are influenced by temperature increases. Sensitivity analysis is done on the model. Numerical simulations predict there exist several scenarios that result in polar bear extinction. When the impact of climate warming is low the population is predicted to die out in 300 years and for higher levels of impact the population can be extinct within 6. The second model is a system of continuous delay differential equations with time-dependent parameters, also influenced by increasing temperatures. The positivity of solutions is found, dependent on sufficient initial conditions. Numerical simulations predicted a threshold value for the impact of temperature. The population always goes extinct if impact is beyond this threshold. The smallest impact predicts extinction in 150+ years and largest in 5 years.

Keywords: Matrix Population, Eigenvalue Sensitivity, Time-Dependent, Delay Differential Equations, Positivity, Polar Bears, Climate Change, Hudson Bay

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List of Abbreviations

WH- Western Hudson Bay

COY- Cubs of the Year

ACIA- Arctic Climate Impact Assessment

GHG- Greenhouse Gases

BPVA- Bayesian Population Viability Analysis

ODE- Ordinary differential equation

DDE- Delay differential equation

Chapter 1

Polar Bears and Climate Change

1.1 Polar Bear Habitat and Life Cycle

Polar bears are the top predators in the Arctic [8, 12, 19]. They have approximately 19 different sub-populations, each differing slightly from the rest based on their location within the Arctic circle [12, 16, 18]. In particular, southern parts of the Arctic have seasonal sea-ice, meaning the ice melts during the summer months and refreezes in time for winter [12]. This changes the habitat of polar bears within a season; going from sea-ice habitat to land habitat [12]. Polar bears are one of the most ice-dependent marine mammals in the Arctic [4]. They depend on the sea-ice for mating, hunting, and travelling which are all crucial components to polar bear survival [8, 11, 7, 22]. The sub-population of interest resides in the southern region of Western Hudson Bay (WH) because this region is one of the first to be experiencing changes in climate [15].

Polar bears spend their time out on the sea-ice in the winter and move on shore in the spring when the ice begins to break-up [15]. During the winter months, bears use the sea-ice to travel, mate and hunt [8, 11, 7, 22]. The main diet of polar bears is ringed seals, bearded seals and occasionally walruses [12, 22, 7]. Ringed seals will lay their dens out on the sea-ice and polar

bears will search for the dens to hunt the baby seals [19, 22]. This is a result of baby seals having a higher fat ratio that is beneficial to the polar bears fat storage [19, 22]. The critical hunting season occurs between April and July and is the time when bears must build up fat stores so they are able to rely on them for survival during the 3-4 month period spent onshore [19, 22, 12].

Polar bears are solitary mammals that spend long durations isolated from others, only coming together during the mating season [9]. All mating occurs out on the sea-ice, with the mating season usually taking place between March and May [22, 9]. During this time males must locate females using their tracks on the ice which can be demanding as great distances often need to be travelled to locate a female [9]. Additionally, males will generally forego feeding during this time [9]. Once a female is pregnant, she will move onshore where she remains in her den for up to 8 months [22, 10, 2]. In particular, pregnant females need to build up their fat stores, as they remain onshore to give birth to cubs [10]. Furthermore, this is incredibly draining on the mother as both she and her cubs must rely on her fat stores for food until cubs are old enough to exit the den [10, 22, 2].

In Hudson Bay, cubs remain with their mother for an average weaning period of 2 years [5, 22, 7, 4]. During this time, cub survival is linked to that of their mother [5, 16]. Consequently, the mother's success at hunting is critical for her own needs and her cubs as she teaches them how to hunt [6]. Cubs of the year (COY) are classified as cubs that are born that year (less than 1 year of age) and *yearlings* are cubs that are 1 year of age [5, 15]. Once yearlings are weaned from their mother, they must now hunt on their own and are responsible for their own survival. These newly independent polar bears are classified as *sub-adults*; they are now surviving on their own but are still unable to reproduce [15, 5, 4].

Prime adults are independent polar bears that are of reproduction age [15, 5, 4]. These

bears have been living and surviving on their own for at least 2 years. Consequently, they are considered to be more stable than both sub-adults and yearlings as they have higher survival rates [15, 7]. Prime adults are able to mate during the mating season, however it is not guaranteed that all bears will find a mate within the season [22, 9]. Since males are able to mate more than once during the season, polar bears are considered to be polygamous [9]. Older and more mature/experienced males are able to win the mate competitions for a female against the younger, more immature males [9, 22].

1.2 Climate Change in the Arctic

Climate change is occurring around the globe and the Arctic is one of the first regions to experience significant changes [14]. Scientists have attributed green house gas (GHG) emissions from human activity, such as burning fossil fuels, as a primary cause [14]. Climate models are universal in associating GHG emissions with the amount of sea-ice present in the Arctic [20]. As a result, the most visible change is occurring to the snow and ice cover on the Arctic Ocean [1]. The general warming trend of increased air temperatures as well as ocean temperatures affects ice cover by reducing ice growth and enhancing ice melt [13, 14]. Furthermore, the reduction of snow and ice results in dark land and water surfaces being present to absorb more radiation than the reflective ice and snow furthering the warming trend [1].

The annual land-surface air temperature recorded in the Arctic Climate Impact Assessment (ACIA) demonstrated a warming trend of $0.09^{\circ}\text{C}/\text{decade}$ in the Arctic [1]. Hudson Bay in particular had increases of $0.3^{\circ}\text{C}/\text{decade}$ [19]. Furthermore, this increasing trend is most pronounced in winter and spring, but all seasons see an increasing trend [1]. In particular, spring air temperatures have increased by $2 - 3^{\circ}\text{C}$ over the past 50 years in Western Hudson Bay (WH) causing ice break-up to occur approximately 3 weeks earlier [15]. Some climate pro-

jection models have predicted that temperature increases could average $2 - 6^{\circ}\text{C}$ over the next century [19]. Stroeve et al. (2007) [20] stated that climate models are in universal agreement that Arctic sea-ice coverage will decline through the 21st century, while other models have predicted the Arctic will be ice-free by the end of the 21st century: with some even predicting as early as 2040 [11, 21]. The impact of climate changes should be thoroughly examined due to the Arctic experiencing climate changes at nearly twice the global rate [21, 14, 1].

1.3 The Impact of Climate Change on Polar Bears

Warmer temperatures in WH have reduced the sea-ice coverage causing the ice-free season to be longer [15]. These changes are having an impact on the habitat of polar bears, which in turn impacts many aspects of their life. The amount of time spent out on the ice is important for their survival [12]. The increases in temperature are causing the sea-ice to break up earlier and are limiting the time available to hunt and mate [12]. Consequently, it is decreasing the amount of time available for both hunting and mating which is having a negative effect on polar bears. It is these negative feedbacks that are damaging to polar bear survival. It is critical to understand this relationship quantitatively, as it can aid in polar bear conservation efforts. Since the bears spend a majority of their year on ice, without this ice the time spent onshore will increase changing the dynamics of polar bear life. Less ice time reduces the opportunities bears can have for hunting seals and impacts the amount of fat storage they are able to build up before fasting [12]. As the total time bears spend on shore increases, the longer they must rely on their fat stores to get them through the summer ice-melt [12].

1.3.1 Mathematical Models of Polar Bear Populations

Previous work has used mark-recapture methods to collect data in order to estimate polar bear populations, survival parameters, growth rates and movement patterns [2, 19, 12]. The data collected in the previous work were analysed for trends. Atkinson and Ramsay found a positive relationship between the mothers fat stores and cub survival [2]. Stirling et al. found earlier sea-ice breakup related to poorer body condition of females and their natality [19]. Parks et al. used satellite collars to track movement on the sea-ice and found that there was decreased movement for bears in Hudson Bay [12]. They relate the cause of this to ice-cover and the duration of the ice season [12].

Rode et al. associated changes in environmental conditions to the body size of polar bears [17]. They examined the relationship between the interannual variation in sea ice availability and several indicators of bear condition (skull size, body mass) and reproduction (litter mass) [17]. Results of the analysis suggested only females in the best body condition are successful at rearing cubs to yearling age [17]. Maternal mass is related to litter mass and both masses declined in bad ice years, as well as the mean skull width and body length of bears [17]. They discovered the biggest declines occurred among younger bears, suggesting those bears are most susceptible to changes [17]. Another similar approach by Molnár et al. used a body composition model using the dynamic energy budget to estimate structural mass, store mass and energy from the body mass and body length of polar bears [10]. The dynamic energy budget model can be used to understand declines in body condition, survival and reproduction.

A few researchers, Hunter et al. , Lunn et al. and Regehr et al. [5, 4, 8, 15] have used discrete matrix models to estimate polar bear populations and examine how they are impacted by climate change. A stochastic matrix population model was used to predict future populations under ice conditions in both Hunter et al. papers [5, 4]. The population model was coupled with a general circulation model to find the population size under the future projections of sea-

ice [5, 4]. They found that in the Southern Beaufort Sea, the number of polar bears declined over the study period and predict that if nothing changes, the population will go extinct [5, 4]. Each of these models used *ice* as a parameter to represent the number of days during the year that were ice-free (less than 50% ice-cover on the open water), to show the impact of climate warming [4]. It was determined that survival depends on *ice* and time, whereas breeding was time-dependent only [4].

Similarly, Lunn et al. used a hierarchical multi-state capture-recapture model [8]. This model was then used to construct a population model that used a Bayesian Population Viability Analysis (BPVA) approach to project potential population outcomes under various sea-ice scenarios [8]. They used hypothetical future sea-ice conditions to project the model to predict future population numbers [8]. The model showed declines in population associated with long-term negative trends in WH [8]. The population change in females was driven by timing of ice break-up and formation and in males was primarily drive by age class due to hunting [8]. The model was able to confirm the link between polar bear survival and sea-ice conditions [8].

The ice conditions are heavily influenced by the temperature: the rate at which ice melts and behaves will depend on the temperature of both the air and water. Knowing this fact, we believe that we should look at how temperature will impact polar bear survival directly rather than indirectly through ice. The melting ice is a direct result of the temperature which is why it is more beneficial to look at the direct cause. Temperature values are easier to project using previous and current temperature trends and therefore can be calculated more directly. Using a population matrix model in discrete time, we can created a time-dependent matrix population model to illustrate the impact of temperature on polar bear populations in Western Hudson Bay. The discrete time model will allow for simplifications and give overall yearly trends for the polar bear population.

Molnár et al. modelled the mating system of polar bears to look for Allee effects [9]. The Allee effect is the relationship between the population density and growth rate of a population [3]. Allee effects are a feature of populations at low densities where the density limits the population growth [3]. With their model, they were able demonstrate mating success was a nonlinear function of the operational sex ratio [9]. This implies that if declines in mating success are caused by male scarcity, a small additional loss of males will cause a rapid reproduction collapse [9]. This approach is different because it looks at polar bears in continuous time rather than discrete time used in the population matrix models. Continuous time allows for the short term dynamics that occur within a population to be modelled explicitly. Hunter et al. said, “Given sufficiently detailed information on both climate and the response of vital rates, the analysis could use a continuous environment model” [4]. This indicates that the use of a continuous time model is desired. Discrete models are missing some information about the short-term behaviours and using continuous time will show more dynamics within the polar bear population. This motivated us to extend the mating model to incorporate dynamics outside of the mating season in order to show how the population behaves throughout the year. The model will also incorporate the impacts of temperature change on the population.

1.3.2 Objective of this Thesis

The main objective of this Thesis is to create two models, one discrete and one continuous, that can be used to represent the population of polar bears under climate change. The discrete time model will allow us to use the yearly population dynamics ignoring short term behaviours in order to determine the long-term behaviour of the polar bear population. The continuous model will allow all the short term behaviours to be incorporated and create a framework for future projects. The goal is to investigate how the increasing temperature in WH will impact the polar population. Through numerical simulations we can predict the future population of polar bears in Western Hudson Bay under various conditions.

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Chapter 2

Time-Dependent Matrix Population Model

2.1 Introduction

Around the globe, the climate is experiencing rapid change [16]. The topic of climate change is one of great relevance as it is posing serious threats to species around the globe [8, 13]. It is projected that the shift in climate will cause major changes to population dynamics, species distributions and biodiversity - just to state a few [8]. In particular, the Southern Arctic is seeing faster changes in climate and is one of the first regions to be experiencing the effects of global warming [14, 19, 8]. Hudson Bay is located in the southernmost part of the Arctic and signs of global warming have been most visible here [14]. The winter and spring air temperatures have been increasing and declines in sea-ice extent, dates of break-up and freeze-up are occurring later as a result [14, 11, 19]. Polar bears are one species among the many in the Arctic that are being impacted by these changes [9, 19, 10].

Polar bears depend on the sea-ice for several aspects of survival which include hunting, breeding and travelling [11, 13, 10, 19, 15, 16, 8]. In Hudson Bay, bears live out on the sea-ice

during the winter months which is approximately 8 months of the year [14]. The remaining summer months are spent onshore when the sea-ice melts [17]. Before arriving onshore, polar bears must hunt seals out on the ice in order to build up fat stores [17]. Once they are onshore, bears must survive off the fat stores until the ice reforms and they can head back out the following winter [12].

Climate warming is having a major impact on the extent of sea-ice and the timing of break-up [8, 16, 15]. The mean air temperatures have been increasing at a rate of 0.3°C per decade in Western Hudson Bay (WH) [17]. Some models predicted that the temperature increase could average $2 - 6^{\circ}\text{C}$ over the next century [17]. As stated by Stroeve et al, “Climate models are in universal agreement that Arctic sea ice extent will decline through the 21st century in response to greenhouse gas [18]”. Others have predicted that it will be ice-free by the end of the 21st century [13]. The delayed autumn and winter ice freeze up will promote increases in surface air temperatures, resulting in the loss of polar bear habitat [18]. With the sea-ice breaking up earlier, bears are forced onshore sooner than expected [8]. This means that the time available to mate and hunt prey is shortened as a result [8, 10]. Polar bears are having to rely on their fat stores for longer periods of time waiting for freeze-up, impacting their overall body condition [10]. It has been shown by other studies that these changes in climate have an impact on both survival and reproduction rates [10, 8]. A large decline in the polar bear population in WH has been linked to climate warming [10, 15].

Using the information known about climate change affecting polar bear survival and reproduction rates, we will create a model to estimate the population growth rate and population size for bears in WH. As Hudson Bay is essentially a closed system, surface air temperatures are one of the principal factors affecting ice conditions [17]. The model will incorporate the changes in survival and reproduction as a result of the increases in temperature, as this is the factor impacting the sea-ice. A matrix population model was a natural choice, as survival and

reproduction are key elements in creating one. Time-dependent parameters were used to depict the changes in temperature as temperature increases with time. Upon both analytic and numerical analysis on the model, we were able to draw conclusions about how the climate change impacts polar bear survival and predict the long-term population of polar bears in the region of WH.

2.2 The Model

A matrix population model was constructed by adapting the life cycle graph provided in Hunter et al. [9]. In Hunter et al., the total polar bear population was divided into 10 different sub-populations with each of the sub-populations corresponding to a particular stage of development. However, we note that certain stages within the polar bear life cycle last more than one year though the changes between those years are minimal. This observation motivated us to combine some stages of development together. More specifically, we will combine the stages of development for sexually immature bears to simplify the model. This simplification of stages brings us some convenience in analysis and numerical simulation without sacrificing the main feature of the age structure of polar bears.

The life cycle graph is shown in Figure 2.1. The model has 4 female compartments ($N_1 - N_4$) which represent the populations of female polar bears at different stages, and 2 male compartments ($N_5 - N_6$) which represent the male populations at different stages of development. Compartments 1 and 5 represent the sub-adult stage of development for females and males respectively. Bears in these compartments are those between 2-4 years in age who are independent from their mothers but are not yet able to reproduce. Bears remain in these two compartments with survival probability P_1 and P_5 and survive and move to the next compartment with probability σ_1 and σ_5 . Compartment 2 represents the population of prime adult females, who are

bears of reproduction age (5+ years) that are available for breeding. Females in this compartment breed with probability β_2 , which is conditional on their survival σ_2 . The probability that a bear does not successfully breed in that season is then given by $(1 - \beta_2)$, also conditional on their survival P_2 . Successful breeding brings female bears to compartment 3, which represents the population of females with cubs of the year (COY). Females that have produced cubs have survival probability σ_3 . Let σ_{L0} be the probability that at least 1 COY survives the first season and β_3 be the probability that a female loses her COY early enough that she can breed again that season. Compartment 4 represents the population of females with yearlings. The mother survives this stage and moves back to compartment 2 to breed again with probability σ_4 . At least 1 yearling cub survives with probability σ_{L1} , which is conditional on the mothers survival. Here f represents the average number of 2-year-old cubs in successful litters. Lastly, compartment 6 is the population of males at reproduction age and they remain in this stage with probability P_6 .

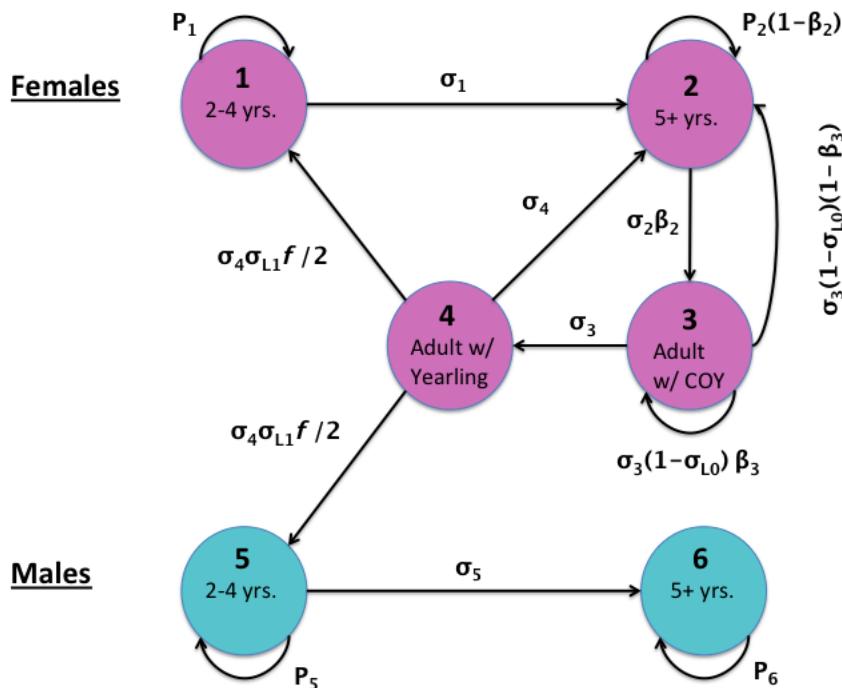


Figure 2.1: Life cycle graph for polar bears

The life cycle graph corresponds to a matrix population model,

$$\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t), \quad (2.1)$$

where

$$\mathbf{N}(t) = [N_1(t), N_2(t), N_3(t), N_4(t), N_5(t), N_6(t)]$$

and

$$\mathbf{A} = \begin{bmatrix} P_1 & 0 & 0 & \frac{\sigma_4\sigma_{L1}f}{2} & 0 & 0 \\ \sigma_1 & P_2(1 - \beta_2) & \sigma_3(1 - \sigma_{L0})(1 - \beta_3) & \sigma_4 & 0 & 0 \\ 0 & \sigma_2\beta_2 & \sigma_3(1 - \sigma_{L0})\beta_3 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{\sigma_4\sigma_{L1}f}{2} & P_5 & 0 \\ 0 & 0 & 0 & 0 & \sigma_5 & P_6 \end{bmatrix} \quad (2.2)$$

is the population projection matrix, $\mathbf{N}(t)$ is the vector giving the populations of polar bears in all six compartments and t is measured in years. A summary of parameters and their descriptions are shown in Table 2.1.

Parameter	Definition
$N_1(t)$	Population of sub-adult females
$N_2(t)$	Population of prime-adult females
$N_3(t)$	Population of females with COY
$N_4(t)$	Population of females with yearlings
$N_5(t)$	Population of sub-adult males
$N_6(t)$	Population of prime-adult males
P_1	Probability of remaining in compartment 1
σ_1	Probability of surviving from compartment 1 to 2
P_2	Probability of remaining in compartment 2
σ_2	Probability of surviving from compartment 2 to 3
σ_3	Probability of surviving from compartment 3 to 4
σ_4	Probability of moving from compartment 4 to 2
P_5	Probability of remaining in compartment 5
σ_5	Probability of moving from compartment 5 to 6
P_6	Probability of remaining in compartment 6
σ_{L0}	Survival probability of a COY litter
σ_{L1}	Survival probability of a yearling litter
β_2	Breeding probability of females
β_3	Breeding probability of females who lose a COY early enough to breed again
f	Average number of cubs in a successful litter

Table 2.1: Descriptions of all parameters used in the model

Matrix models of the form (2.1) have been extensively and intensively studied by many researchers for various species, see Caswell et al. (2004), Crouse et al. and others cited within [2, 4, 7, 5, 3]. However, in reality, certain model parameters are not necessarily constant and can change or fluctuate with time. When considering such time dependence, (2.1) is modified to,

$$\mathbf{N}(t+1) = \mathbf{A}(t) \mathbf{N}(t), \quad (2.3)$$

where $\mathbf{A}(t)$ is the projection matrix with time-dependent parameters and $\mathbf{N}(t)$ is still the vector giving the populations of bears in all compartments. Analysis of such a non-autonomous system [e.g. (2.3)] is much harder than that of an autonomous system [e.g. (2.1)]. In Section 2.3, by analyzing (2.1), we investigate the impact of the model parameters on the population dynamics. In Section 2.4, by incorporating real parameter values we verify and support the

analytic findings. In Section 2.5, by specifying some particular form of the time dependent parameters, we numerically explore the population dynamics; particularly we will examine the effect of climate change by properly choosing the time-dependent functions.

2.3 Analytic Analysis

2.3.1 Constant Parameter Model

We begin by looking at the special case in which the parameters have constant values. This case will be used as a base case for comparisons.

Long-Term Population Dynamics

The autonomous model (2.1) can be solved explicitly by eigenvector expansion. Let $\lambda_i, i = 1, \dots, 6$ be the eigenvalues of the matrix \mathbf{A} and v_i^*, w_i be the complex conjugate transpose of the left eigenvector and unit vector of the right eigenvector of \mathbf{A} corresponding to λ_i . Assume that the initial value $\mathbf{N}(0)$ has the expansion $\mathbf{N}(0) = \sum_{i=1}^6 c_i w_i$. The solution of (2.1) is given by

$$\mathbf{N}(t) = \mathbf{A}^t \mathbf{N}(0) = \sum_{i=1}^6 c_i w_i \lambda_i^t. \quad (2.4)$$

The coefficient c_i can actually be determined as $c_i = \mathbf{N}(0) v_i^*$.

Note that \mathbf{A} (2.2) is a non-negative matrix. We first recall some results on the eigenvalues and eigenvectors for non-negative matrices, which are generally referred to as the Perron-Frobenius Theorem. The most classic one is the following.

Theorem 2.1(Caswell [1]) Assume that A is an $s \times s$ non-negative square matrix and let $\lambda_i, i = 1, \dots, s$ be all the eigenvalues of A . If A is *irreducible*, then there is a real $\lambda_j > 0$ with corresponding left and right eigenvectors $v_j > 0$ and $w_j > 0$, satisfying $|\lambda_i| < \lambda_j$ for $i = 1, 2, \dots, s$

with $i \neq j$.

The eigenvalue λ_j in the above theorem is referred to as the dominant eigenvalue. There are many ways to determine whether a matrix is irreducible, and we will employ the following theorem from Caswell [1].

Theorem 2.2 (Caswell [1]) Assume that A is an $s \times s$ non-negative square matrix. Then, A is *irreducible* if and only if $(I + A)^{s-1}$ is positive.

Now, for the matrix \mathbf{A} in our model given by (2.2), direct calculations give

$$(\mathbf{I} + \mathbf{A})^5 = \begin{bmatrix} + & + & + & + & 0 & 0 \\ + & + & + & + & 0 & 0 \\ + & + & + & + & 0 & 0 \\ + & + & + & + & 0 & 0 \\ + & + & + & + & (1 + P_5)^5 & 0 \\ + & + & + & + & + & (1 + P_6)^5 \end{bmatrix}.$$

which is obviously not positive since there are several zeros in the upper-right block. Thus, the matrix \mathbf{A} in (2.1) is not reducible and hence, the results in Theorem 2.1 cannot be applied. For a non-negative reducible matrix, there is the following weaker version of the Perron-Frobenius Theorem.

Theorem 2.3 (Caswell [1]) Assume that A is an $s \times s$ non-negative square matrix and let $\lambda_i, i = 1, 2, \dots, s$ be all the eigenvalues of A . If A is *reducible*, then there exists a real eigenvalue $\lambda_j \geq 0$ with the corresponding left and right eigenvectors $v_1 \geq 0$ and $w_1 \geq 0$, satisfying $|\lambda_i| \leq \lambda_j$ for $i = 1, 2, \dots, s$ with $i \neq j$.

Without loss of generality, we can always assume (it is just a matter of rearranging the order) that $\lambda_1 = \lambda_j$.

Note that in Theorem 2.3, there is no guarantee that

$$|\lambda_i| < \lambda_1 \text{ for } i = 1, 2, \dots, s; \text{ and } w_1 > 0. \quad (2.5)$$

These two properties are important and thus, we would like to explore further for a reducible non-negative matrix. To this end, we recall some result from Caswell [1] and Gantmacher [6].

A matrix of the form

$$\mathbf{A} = \begin{bmatrix} B_1 & 0 \\ \hline B_{21} & B_2 \end{bmatrix},$$

is said to be in normal form if each matrix block on the diagonal is irreducible [1, 6]. For a matrix in the above normal form, B_1 is isolated from B_2 but B_2 is not isolated from B_1 as it depends on one or more of the compartments in B_1 . The conditions for the long-term dynamics of reducible matrices states that $w_1 > 0$ if and only if λ_1 is an eigenvalue of the isolated block and not the non-isolated block [1, 6].

Our matrix \mathbf{A} in (2.1) can be subdivided as shown with

$$\mathbf{A} = \left[\begin{array}{cccc|cc} P_1 & 0 & 0 & \frac{\sigma_4\sigma_{L1}f}{2} & 0 & 0 \\ \sigma_1 & P_2(1-\beta_2) & \sigma_3(1-\sigma_{L0})(1-\beta_3) & \sigma_4 & 0 & 0 \\ 0 & \sigma_2\beta_2 & \sigma_3(1-\sigma_{L0})\beta_3 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & \frac{\sigma_4\sigma_{L1}f}{2} & P_5 & 0 \\ \hline 0 & 0 & 0 & 0 & \sigma_5 & P_6 \end{array} \right],$$

such that

$$\mathbf{A} = \begin{bmatrix} B_1 & 0 & 0 \\ \hline B_{21} & B_2 & 0 \\ \hline 0 & B_{32} & B_3 \end{bmatrix},$$

where

$$\begin{aligned}
 B_1 &= \begin{bmatrix} P_1 & 0 & 0 & \frac{\sigma_4 \sigma_{L1} f}{2} \\ \sigma_1 & P_2(1 - \beta_2) & \sigma_3(1 - \sigma_{L0})(1 - \beta_3) & \sigma_4 \\ 0 & \sigma_2 \beta_2 & \sigma_3(1 - \sigma_{L0})\beta_3 & 0 \\ 0 & 0 & \sigma_3 & 0 \end{bmatrix} \\
 B_{21} &= \begin{bmatrix} 0 & 0 & 0 & \frac{\sigma_4 \sigma_{L1} f}{2} \\ 0 & 0 & 0 & 0 \end{bmatrix} \\
 B_2 &= \begin{bmatrix} P_5 \end{bmatrix} \\
 B_{32} &= \begin{bmatrix} \sigma_5 \end{bmatrix} \\
 B_3 &= \begin{bmatrix} P_6 \end{bmatrix}.
 \end{aligned} \tag{2.6}$$

B_1 for our model is isolated, as it only depends on compartments 1 through 4. However, B_2 and B_3 are non-isolated as they depend on input from compartments 4 and 5 respectively. Therefore, for (2.5) to hold the dominant eigenvalue must be from the irreducible B_1 matrix. If the largest eigenvalue is from B_2 or B_3 than the female population (compartments 1-4) will go to zero. This can be seen easily since the population cannot growth when $\lambda_1 < 1$ and the eigenvalues of B_2 and B_3 are given by P_5 and P_6 respectively, where P_i are probabilities between (0, 1). Thus, it confirms the properties in (2.5) for the matrix \mathbf{A} in (2.1) when the dominant eigenvalue λ_1 is an eigenvalue from B_1 .

When (2.5) holds, the eigenvalue λ_1 is referred to as the population growth rate. Based on the above analysis, our model (2.1) has a dominant eigenvalue λ_1 which gives the long-term growth rate for the population, with the corresponding w_1 strictly positive which represents the

long-term stable stage structure. This can be seen by rewriting (2.4) as

$$\begin{aligned}
 \mathbf{N}(\mathbf{t}) &= A^t \mathbf{N}(\mathbf{0}) \\
 &= A^t (c_1 w_1 + c_2 w_2 + c_3 w_3 + c_4 w_4 + c_5 w_5 + c_6 w_6) \\
 &= c_1 A^t w_1 + c_2 A^t w_2 + c_3 A^t w_3 + c_4 A^t w_4 + c_5 A^t w_5 + c_6 A^t w_6 \\
 &= c_1 \lambda_1^t w_1 + c_2 \lambda_2^t w_2 + c_3 \lambda_3^t w_3 + c_4 \lambda_4^t w_4 + c_5 \lambda_5^t w_5 + c_6 \lambda_6^t w_6 \\
 &= \lambda_1^t \left(c_1 w_1 + c_2 \left(\frac{\lambda_2}{\lambda_1} \right)^t w_2 + c_3 \left(\frac{\lambda_3}{\lambda_1} \right)^t w_3 + c_4 \left(\frac{\lambda_4}{\lambda_1} \right)^t w_4 + c_5 \left(\frac{\lambda_5}{\lambda_1} \right)^t w_5 + c_6 \left(\frac{\lambda_6}{\lambda_1} \right)^t w_6 \right).
 \end{aligned}$$

Since λ_1 is the dominant eigenvalue, the above shows for large t , $\mathbf{N}(\mathbf{t})$ can be approximated by,

$$\mathbf{N}(\mathbf{t}) \approx c_1 \lambda_1^t w_1. \quad (2.7)$$

Sensitivity and Elasticity

Eigenvalue sensitivity is used to measure the effect that changes in parameters have on population growth. This is important for the model as it allows us to determine what changes in parameters have the biggest impact on the population growth rate, λ_1 . If we are able to see what parameters are responsible for the largest changes, we can better understand which polar bear stages will be most sensitive to the temperature changes.

The sensitivity of λ_1 to a given parameter π is given by $\frac{\partial \lambda}{\partial \pi}$. Let $v = (v_1, v_2, \dots, v_6)$ and $w = (w_1, w_2, \dots, w_6)$ be the left and right eigenvectors corresponding to λ_1 , scaled so that $v^T w = <$

$v, w \geq 1$. Then by $\lambda_1 = \lambda_1 v^T w = v^T A w$, we obtain

$$\begin{aligned}\frac{\partial \lambda}{\partial \pi} &= \frac{\partial v^T}{\partial \pi} A w + v^T \frac{\partial A}{\partial \pi} w + v^T A \frac{\partial w}{\partial \pi} \\ &= \frac{\partial v^T}{\partial \pi} \lambda_1 w + v^T \frac{\partial A}{\partial \pi} w + \lambda_1 v^T \frac{\partial w}{\partial \pi} \\ &= v^T \frac{\partial A}{\partial \pi} w + \lambda_1 \frac{\partial}{\partial \pi} (v^T w) \\ &= v^T \frac{\partial A}{\partial \pi} w + \lambda_1 \frac{\partial}{\partial \pi} (1) \\ &= v^T \frac{\partial A}{\partial \pi} w\end{aligned}\tag{2.8}$$

which gives the sensitivity of λ_1 to π where the derivative $\frac{\partial A}{\partial \pi}$ is a matrix whose entries are $\frac{\partial a_{ij}}{\partial \pi}$.

If $\pi = a_{ij}$, equation 2.8 is simplified to

$$\frac{\partial \lambda}{\partial a_{ij}} = v_i w_j.\tag{2.9}$$

Elasticity of eigenvalues is similar to sensitivity, however, it looks at changes proportionally rather than absolutely. Elasticities are beneficial when the parameters in the model are of different scales. For example, if a model contains survival probabilities, they are restricted to be between 0 and 1. If the model also includes the average number of cubs born this value can sometimes be much larger than one. For this reason, the elasticity would be best to use and elasticity can be calculated using

$$E_\pi = \frac{\pi}{\lambda} \frac{\partial \lambda}{\partial \pi}.\tag{2.10}$$

2.4 Numerical Analysis

2.4.1 Calculating Parameter Values

A majority of the parameter values used for this model are found in the Environment Canada Research report by Lunn et al. [11], with the exception of β_3 . The survival probabilities, σ_1, P_1, σ_5 and P_5 are not directly from the report but can be calculated using the survival probabilities

found within the report. The survival probability provided in the report included independent yearlings to 4-year-old polar bears. We assume that there are few independent yearlings, since most bears are weaned at 2 years of age. Then the probability provided was for 3 stages: 2-year-old bears, 3-year-old bears and 4-year-old bears. The probability of remaining in the sub-adult stage (P_1 and P_5) can be given as 2/3 of the probability provided. Then the probability of surviving to move to the compartment of bears age 5 (σ_1 and σ_5) can be given as 1/3 of the probability provided.

The parameter β_3 is taken from Hunter et al. [9]. Since the probability of this event occurring is so small, we assume it would be the same for the WH polar bear population. The parameters, f , σ_{L0} and σ_{L1} , are not taken directly from Lunn et al. [11], but can be calculated using the parameters within the report and applying the method shown in Hunter et al. [9].

We begin by assuming that the distribution of litter size is given by $\mathbf{c} = (c_1, c_2)$ where c_i is the probability of having a litter of size i . We assume that the maximum is two cubs per litter, since triplet litters are rare [9]. The probability of losing the whole COY litter can then be estimated by

$$1 - \sigma_{L0} = (1 - s_0)c_1 + (1 - s_0)^2c_2, \quad (2.11)$$

where s_0 is a measure of COY survival. Equation 2.11 can be solved for σ_{L0} , given c_1, c_2 and s_0 , which are provided in Lunn et al. [11]. The size distribution of the yearling litter, which is conditional on COY litter survival can then be given by,

$$\begin{aligned} y_1 &= \frac{[c_1 s_0 + 2c_2 s_0(1 - s_0)]}{\sigma_{L0}} \\ y_2 &= \frac{c_2 s_0^2}{\sigma_{L0}} \end{aligned} \quad . \quad (2.12)$$

The probability of losing the whole yearling litter between compartment 4 and 1 (or 4 and 5) is

$$1 - \sigma_{L1} = (1 - s_1)y_1 + (1 - s_1)^2y_2, \quad (2.13)$$

where s_1 is a measure of yearling survival. This can be solved given s_1 also found in Lunn et al. [11] for σ_{L1} . Similarly, the size distribution of bears moving into compartment 1 and 5 (2 years old) is conditional on the survival of the yearling litter and is given by,

$$\begin{aligned} z_1 &= \frac{[y_1 s_1 + 2y_2 s_1(1 - s_1)]}{\sigma_{L1}} \\ z_2 &= \frac{y_2 s_1^2}{\sigma_{L1}} \end{aligned} \quad . \quad (2.14)$$

The number of new bears entering both compartment 1 and 5 can then be calculated with

$$f = z_1 + 2z_2. \quad (2.15)$$

The parameter values f , σ_{L0} and σ_{L1} are calculated using the method above. We want to note s_1 was chosen from the female cub survival average rather than male cub survival. We also note β_2 and P_6 were the given probabilities for bears between 10-19 years of age rather than 5-9 years of age. We chose this range because it covered a broader range of age values. The parameter values used for the constant matrix model are summarized in Table 2.2.

Parameter	Value
σ_1	0.273
P_1	0.547
σ_2	0.94
P_2	0.94
σ_3	0.94
σ_{L1}	0.755
σ_{L0}	0.676
σ_5	0.25
P_5	0.5
P_6	0.90
β_2	0.31
f	1.1456
c_1	0.53
c_2	0.47
s_0	0.56
s_1	0.71

Table 2.2: Parameter values for constant population matrix

2.4.2 Dominant Eigenvalue, Sensitivity and Elasticity

The eigenvalues of the matrices A , B_1 , B_2 and B_3 were calculated and are shown in Table 2.3.

Matrix	Eigenvalue	Value
A	λ_1	1.0354
	λ_2	0.90
	λ_3	0.50
	λ_4	$-0.1323 + 0.4656i$
	λ_5	$-0.1323 - 0.4656i$
	λ_6	0.4552
B_1	λ_1	1.0354
	λ_2	$-0.1323 + 0.4656i$
	λ_3	$-0.1323 - 0.4656i$
	λ_4	0.4552
B_2	λ_1	0.50
B_3	λ_1	0.90

Table 2.3: Eigenvalues of matrix A , B_1 , B_2 and B_3

The dominant eigenvalue of \mathbf{A} has the value, $\lambda_1 = 1.0354$. It is clear that this eigenvalue is the same dominant eigenvalue from B_1 . Since B_1 is an isolated sub-matrix of \mathbf{A} the population's stable stage distribution, w_1 is strictly positive and is determined to be

$$w_1 = [0.1867, 0.8519, 0.2470, 0.2243, 0.1704, 0.3146]^T. \quad (2.16)$$

The sensitivity of λ_1 to changes in each parameter are calculated. The results of the sensitivity analysis are displayed in Figure 2.2. It can be seen that the population growth rate is most sensitive to changes in P_2 , which is the probability of remaining in compartment 2. Due to the fact compartment 2 is the stage where breeding occurs, the population growth should be sensitive to changes during this stage. If female polar bears are not remaining in this compartment to reproduce, the population would not be able to grow. The growth rate is also sensitive to σ_3 and σ_2 . These are the survival probabilities of females with COY and pregnant females. The population growth would be sensitive to changes in these parameters as cub survival during these stages is dependent on the mother, with successful cubs growing the population [8]. The population growth rate is also sensitive to changes in σ_4 and β_2 which are the survival probability of females returning to breed and the breeding probability, respectively. It should be noted that survival of males has no change on population growth. This is because this model does not explicitly incorporate males into the breeding success, which can be seen as the male compartments are decoupled.

The elasticities of λ_1 to each parameter are shown in Figure 2.3. The dominant eigenvalue is most elastic to changes in P_2 . Again, this is reasonable since for population growth to occur we need female bears to be in the reproduction stage. The growth rate is also elastic to changes in σ_3 and σ_2 . This is explained by the requirement of mothers to have COY that survive to yearlings. This can be looked at as having a successful litter. The population growth rate is also elastic to changes in σ_4 and σ_{L0} , the survival probability of females returning to the

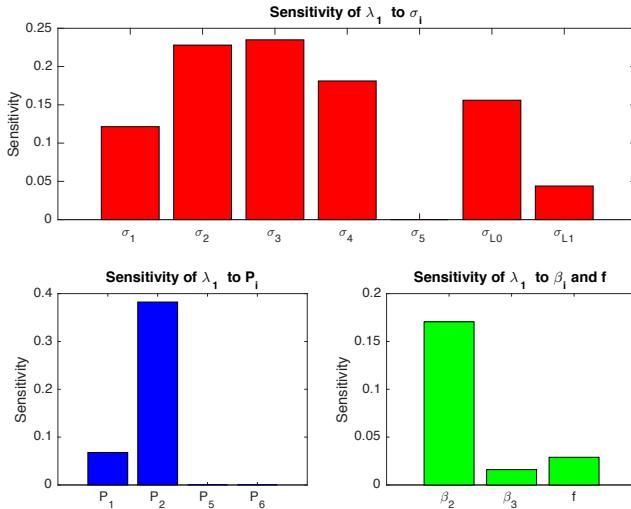


Figure 2.2: Sensitivity of λ_1 for all parameters. Top: The sensitivity of λ_1 to the survival probabilities σ_i . Bottom Left: The sensitivity of λ_1 to the survival probabilities P_i . Bottom Right: The sensitivity of λ_1 to the breeding probabilities β_i and average number of cubs f .

breeding stage and COY litter survival. It is noted that the elasticity to changes in β_2 is not as predominant as the sensitivity was. This implies that, proportionally, the changes are not as big as the absolute changes were.

2.4.3 Solution of Constant Matrix

The solution of the matrix model (2) was calculated using (4). The initial condition was chosen as

$$\mathbf{N}(\mathbf{0}) = \begin{bmatrix} 100 \\ 300 \\ 100 \\ 100 \\ 100 \\ 300 \end{bmatrix}.$$

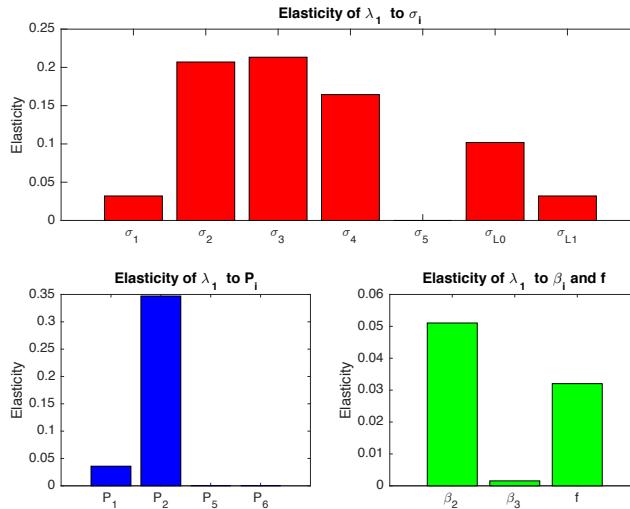


Figure 2.3: Elasticity of λ_1 to all parameters. Top: The elasticity of λ_1 to the survival probabilities σ_i . Bottom Left: The elasticity of λ_1 to the survival probabilities P_i . Bottom Right: The elasticity of λ_1 to the breeding probabilities β_i and average number of cubs f .

This condition was chosen using the polar bear population data provided on polar bears in Western Hudson Bay [14, 11]. The graph of the solution is shown in Figure 2.4. The stable stage distribution was calculated using the initial condition and equation (2.7) and is given by,

$$\mathbf{N}(t) = c_1 \lambda_1^t w_1 = (391.24)(1.0354)^t \begin{bmatrix} 0.1867 \\ 0.8519 \\ 0.2470 \\ 0.2243 \\ 0.1704 \\ 0.3146 \end{bmatrix}. \quad (2.17)$$

The stable stage distribution (2.17) is plotted in Figure 2.5 for comparison to Figure 2.4.

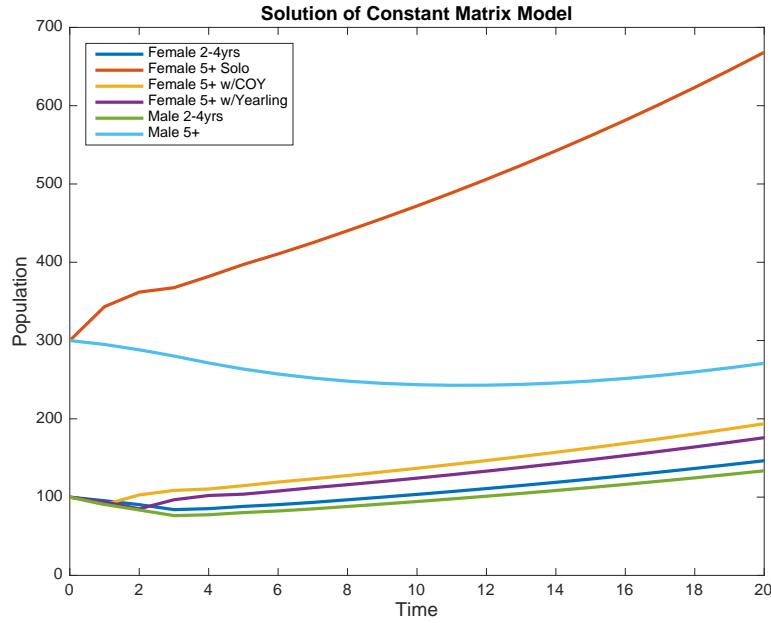


Figure 2.4: Solution curves for constant matrix model (2.1) with all parameter values taken from Table 2.2.

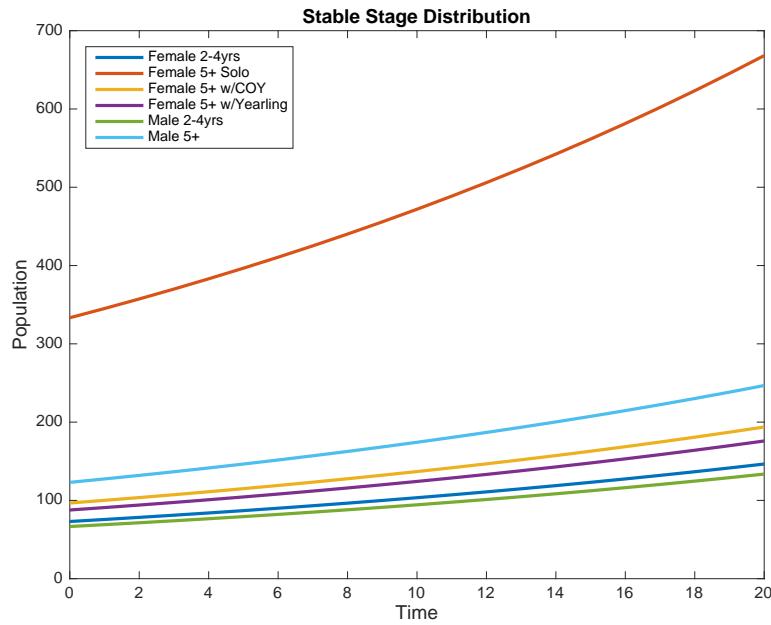


Figure 2.5: Plot of the stable stage distribution given by (2.17) using all the parameter values from Table 2.2

In Figure 2.4, it can be seen that the population is growing overall. There are some small declines occurring around 1-3 years for some of the stages. This is due to the complex eigenvalues dominating during this time, demonstrating the short-term dynamics. It can be seen that for larger values of time, the dominant eigenvalue takes over and population growth follows the stable stage distribution. Comparing Figure 2.4 with Figure 2.5, it is clear that the population is indeed following this distribution.

2.5 Time-Dependent Parameter Model

As mentioned in Section 2.2, the model for time-dependent parameters was given by

$$\mathbf{N(t+1)} = \mathbf{A(t)} \mathbf{N(t)},$$

where $\mathbf{A(t)}$ is the projection matrix with time-dependent parameters and $\mathbf{N(t)}$ the vector giving the number of bears in each compartment. This section will discuss how the form of the time-dependent parameters was chosen.

To start, we know that temperature in the Arctic is declining - causing sea-ice to melt, in turn affecting the population dynamics of polar bears. We begin by assuming that the changes in temperature will have a negative impact. This assumption helps ensure that the time-dependent parameter will be decreasing with time.

Next, we let the current temperature be a function of time such that,

$$T(t) = T_0 + at^r, \quad (2.18)$$

where a is the average temperature increase/decrease per year, T_0 is the average initial temper-

ture and r determines the concavity of temperature increase (ie. $r = 1$ is linear). Then, we let the time-dependent parameter, $\pi(t)$, be a decreasing function of temperature,

$$\pi(t) = \pi_0 - g(T(t) - T_0), \quad (2.19)$$

where π_0 is the initial parameter value and $g(T(t) - T_0)$ is an increasing function of temperature change. The increasing function was chosen to have the general form,

$$g(u) = ku^\alpha, \quad (2.20)$$

where α represents the impact of temperature change on parameters and k is an important scaling factor. The value of k was chosen to ensure survival and breeding probabilities remained non-negative for a particular amount of time. Substituting (2.18) and (2.19) into (2.20) gives,

$$\pi(t) = \pi_0 - k(at^r)^\alpha. \quad (2.21)$$

This is the form that each time dependent parameter took on. The values for r and α were varied to see how they impacted population growth. For $r < 1$ temperatures increase follow a concave down increase where at first the increase is rapid then levels out as time goes on. When $r = 1$ the increase is linear and for $r > 1$ increases follows a concave up pattern where increases are small at first then rapid as time goes on. The relationship between $\pi(t)$ and r is shown in Figure 2.6. The point of intersection shows when the temperature values are equal. Similar to r , when $\alpha < 1$ the impact temperature has on parameters is large at first and slows down with time and when $\alpha = 1$ the impact is linear over time. Lastly, for $\alpha > 1$ the impact is slower at the beginning and increases rapidly as time increases.

The time-dependent parameters were added into the model in 3 cases. The first case, only survival parameters (σ_i and P_i) were considered time-dependent. For the second case, both

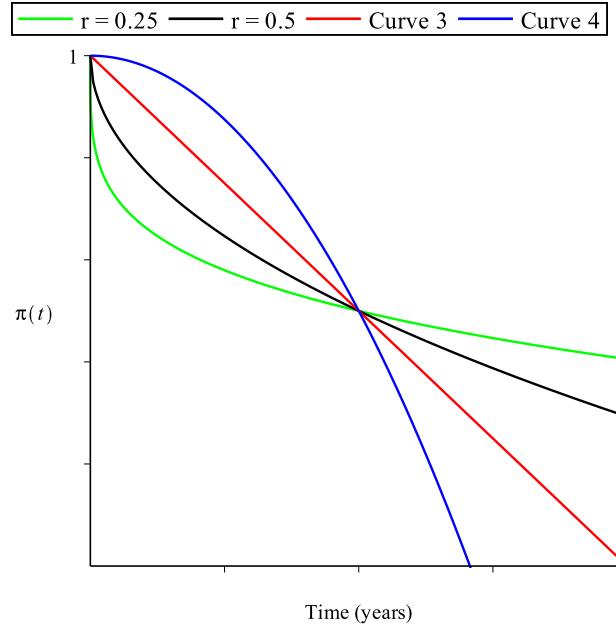


Figure 2.6: Plot demonstrating how the value of r (related to temperature increase) impacts parameters π with increasing time

survival and breeding parameters were considered time-dependent. The final case considers when some parameters are affected by temperature differently at each stage of development. This case is of most interest as it has been shown that yearlings and sub-adults are the most affected by temperature changes.

2.5.1 Case 1 - Results

For this case, the time dependent parameters were $\sigma_i(t)$ and $P_i(t)$. All other parameters remained as constants. The solution curves were calculated using

$$N(t) = \prod_{i=1}^t A(t-i)N(0). \quad (2.22)$$

The constant parameter values used are given in Table 2.2 as well as the initial values for the time-dependent parameters. For all three cases, the average increase in temperature was set at

$a = 0.03$, from the estimated temperature increase of 0.3° C per decade [17]. The parameters α and r took on the values $\{0.25, 0.5, 1, 2\}$ and each value was varied. The parameter k was set as $k = 0.1$. This allowed the model to remain valid for a minimum of 6 years in extreme cases (both $\alpha = 2$ and $r = 2$). All time-dependent parameters had the same k, α and r values.

The solution curves of the time-dependent matrix model for case 1 are shown in Figures 2.7 - 2.10. Figure 2.7 displays the population curves when $r = 0.25$ and α varies. When $\alpha = 0.25$ the population grows for a short period of time but then declines as time goes on and reaches extinction around 180 years. Similarly, the population grows then declines for large values of time when $\alpha = 0.5$ and reaches extinction around 1000 years. The population growth follows an exponential pattern for both $\alpha = 1$ and 2 .

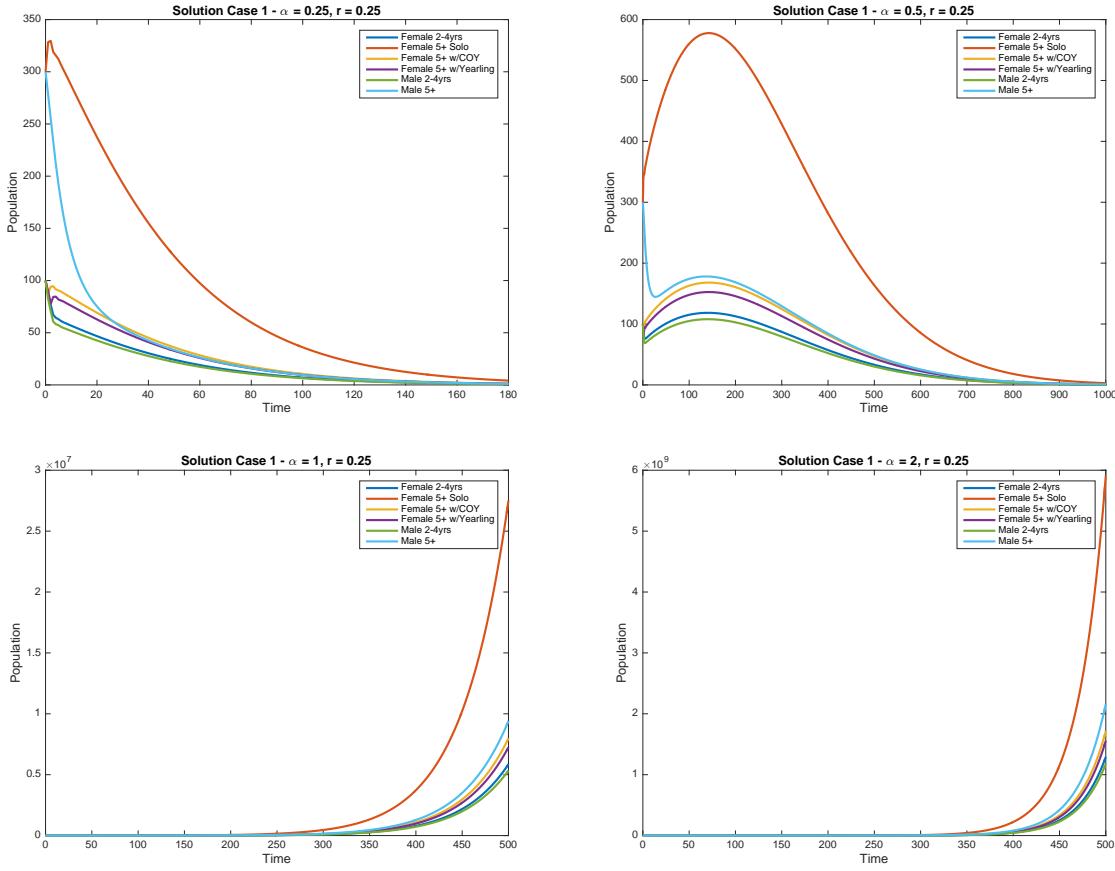


Figure 2.7: Solution curves for Case 1 where only survival rates are time-dependent with $k = 0.1$, $r = 0.25$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

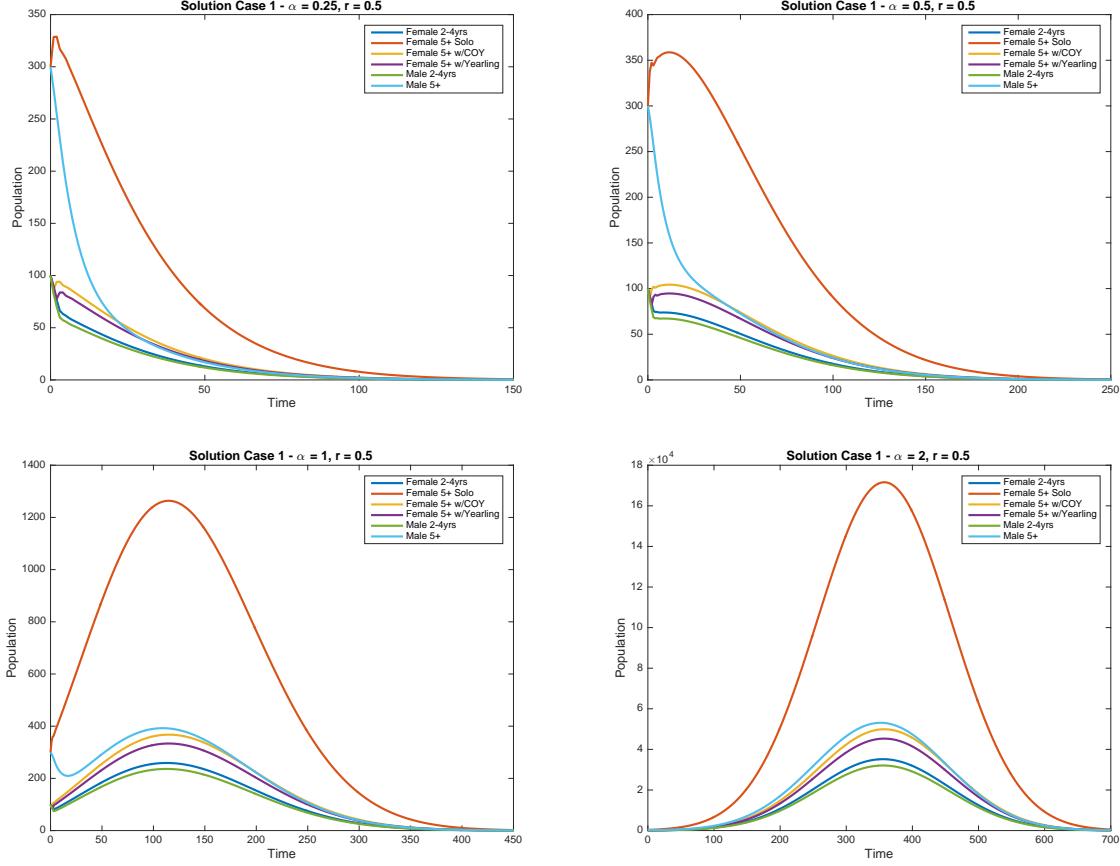


Figure 2.8: Solution curves for Case 1 where only survival rates are time-dependent with $k = 0.1$, $r = 0.5$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

Figure 2.8 shows the situation where $r = 0.5$ and α varies. For all scenarios of α , the population tends to zero. The time scale at which this occurs is different for each α . The population goes to extinction after approximately 150 years, 250 years, 450 years and 700 years for $\alpha = 0.25, 0.5, 1$ and 2 , respectively. The population growth reaches a peak before it declines for all values of α . These peaks occur around 10, 20, 125 and 350 years for $\alpha = 0.25, 0.5, 1$ and 2 , respectively. We note that for $\alpha = 2$, the females of breeding age reach a population of 170,000 which is biologically unrealistic. In Figure 2.9, the case when $r = 1$ and α varies is presented. The population tends to zero for all values of α . The population growth reaches a peak before declining around 8, 10, 15 and 20 years for $\alpha = 0.25, 0.5, 1$ and 2 and time to

extinction is 80, 70, 60 and 50 years, respectively.

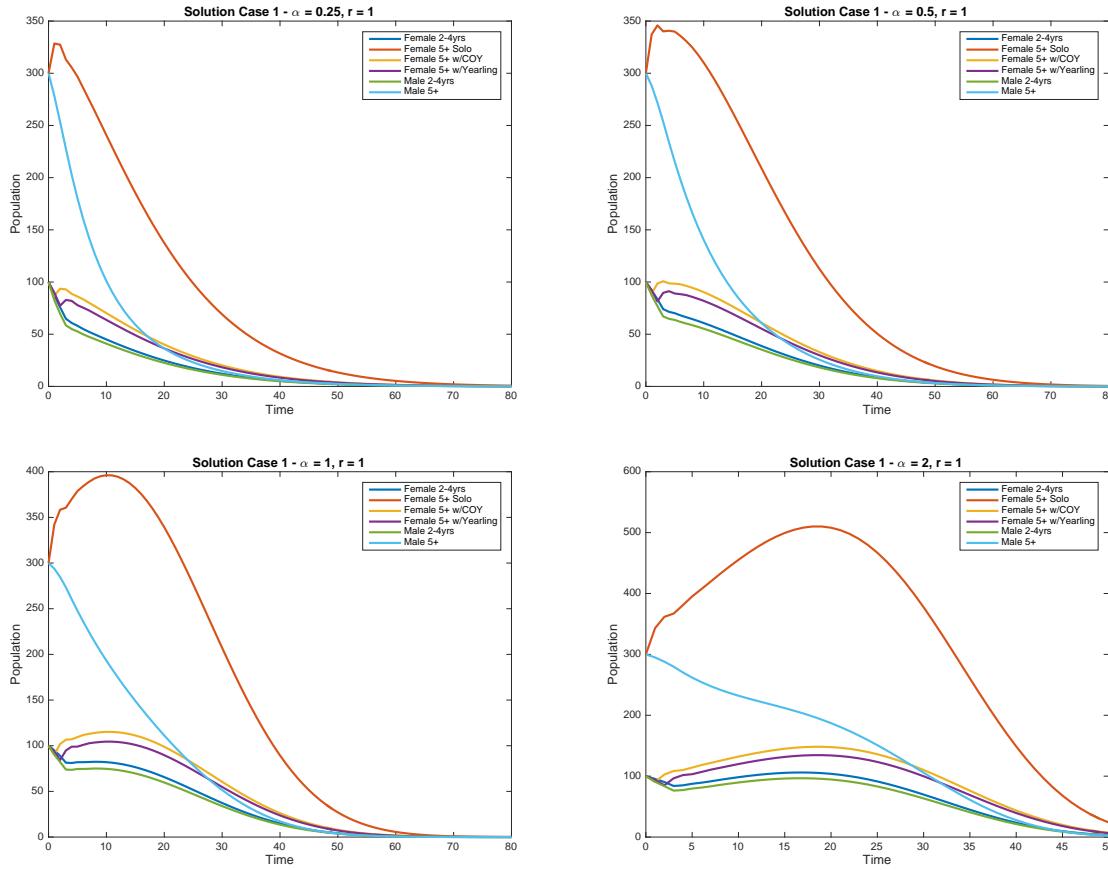


Figure 2.9: Solution curves for Case 1 where only survival rates are time-dependent with $k = 0.1$, $r = 1$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

The results for when $r = 2$ and α is varied are shown in Figure 2.10. In all scenarios, the parameter $\sigma_5(t)$ is the first to reach zero. The amount of time each case remains valid can be seen by observing the time axis. The population growth appears to be tending toward zero for all cases of α . Once $\sigma_5(t)$ reaches zero, the male population will rapidly decline, in turn causing extinction.

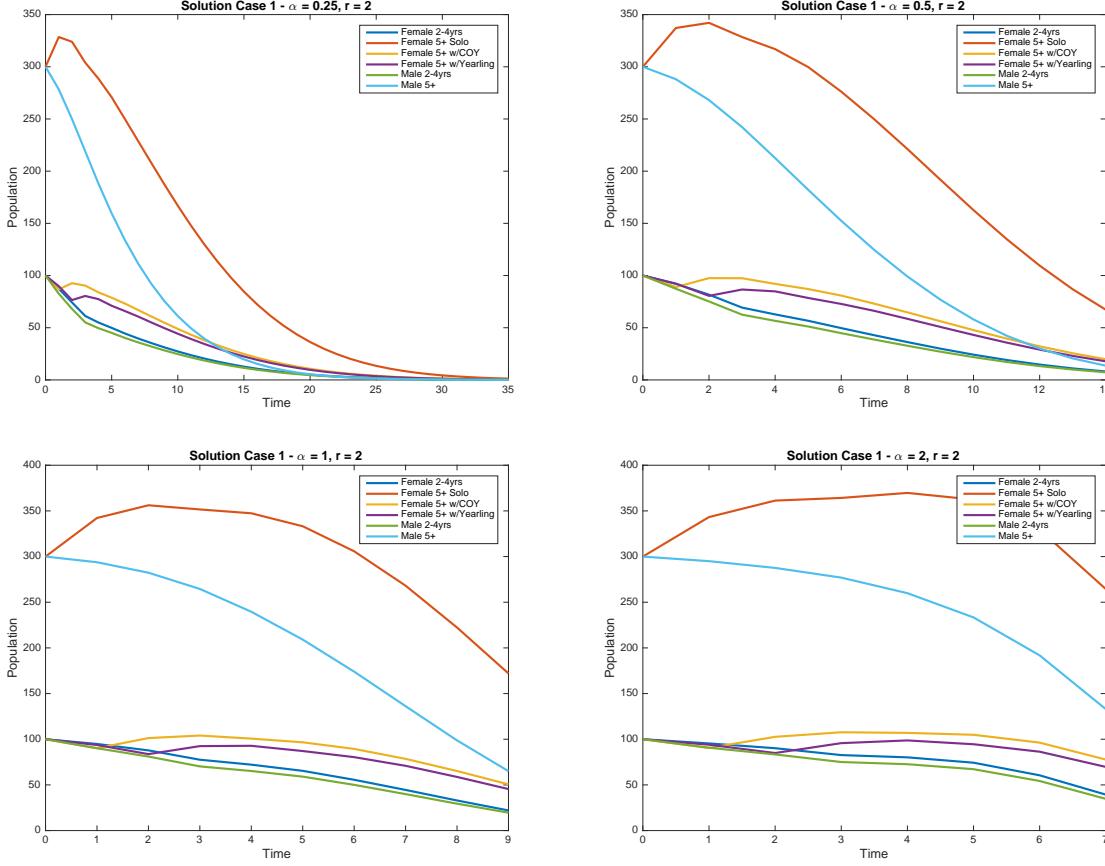


Figure 2.10: Solution curves for Case 1 where only survival rates are time-dependent with $k = 0.1$, $r = 2$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

2.5.2 Case 2 - Results

For the second case, we look at survival and breeding impacted by temperature. The time-dependent parameters were $\sigma_i(t)$, $P_i(t)$ and $\beta_2(t)$ and all other parameters remained constant. We assumed breeding probability β_3 remained a constant. This was due to the fact the probability is already small and would go to zero too rapidly, not allowing the model to stay valid long-enough to see long-term population dynamics. The parameter f was also left as a constant since it was assumed if the litters were successful, they would still produce the average number of 1.5 cubs. Both of these assumptions are justified by noting that population growth was least

sensitive to changes in β_3 and f . The solution curves were also calculated using Equation 2.22. Initial and constant parameter values were taken from Table 2.2. The parameters a, k, r and α were the same for all time-dependent parameters and took on the same values as those used in Case 1.

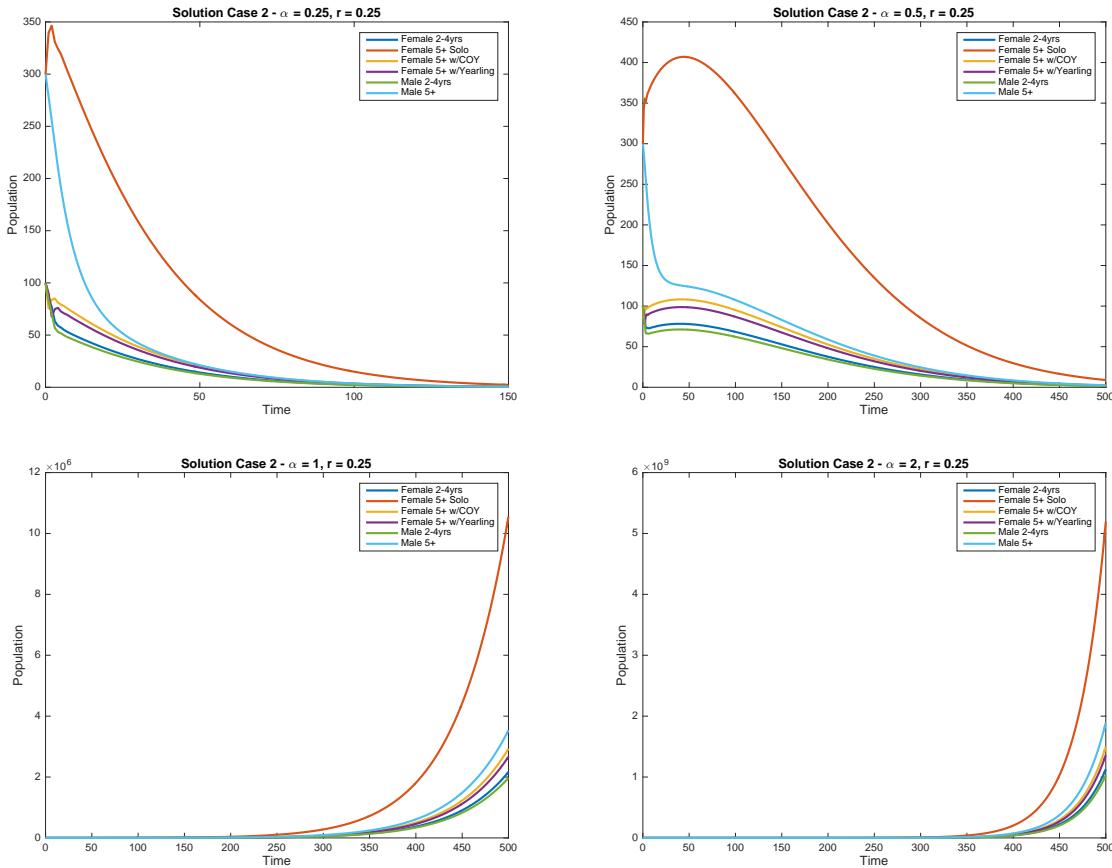


Figure 2.11: Solution curves for Case 2 where both survival and breeding are time-dependent with $k = 0.1$, $r = 0.25$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

The results of the model for Case 2 are shown in Figures 2.11 - 2.14. For Figure 2.11 $r = 0.25$ and α varies. The population growth is small and tends to zero after 150 years when $\alpha = 0.25$. When $\alpha = 0.5$ the population growth reaches a peak around 70 years and then declines steadily until it reaches extinction at approximately 500 years. For both $\alpha = 1$ and 2

the population growth is exponential for all time.

The cases for $r = 0.5$ and α varying are displayed in Figure 2.12. For all α values the population peaks then decreases to zero. The peaks occur at different times for each respective α . When $\alpha = 0.25$ the peak occurs after 10 years and approaches zero after 100. The peak occurs at approximately 30 years and declines to zero around 180 years for $\alpha = 0.5$ and for $\alpha = 1$ the peak is at 100 and tends to zero after 350 years. Lastly, the population reaches its maximum growth around 300 years and declines to zero after 600 years for $\alpha = 2$. We note that the population of breeding females is around 70,000 bears - which does not make biological sense.

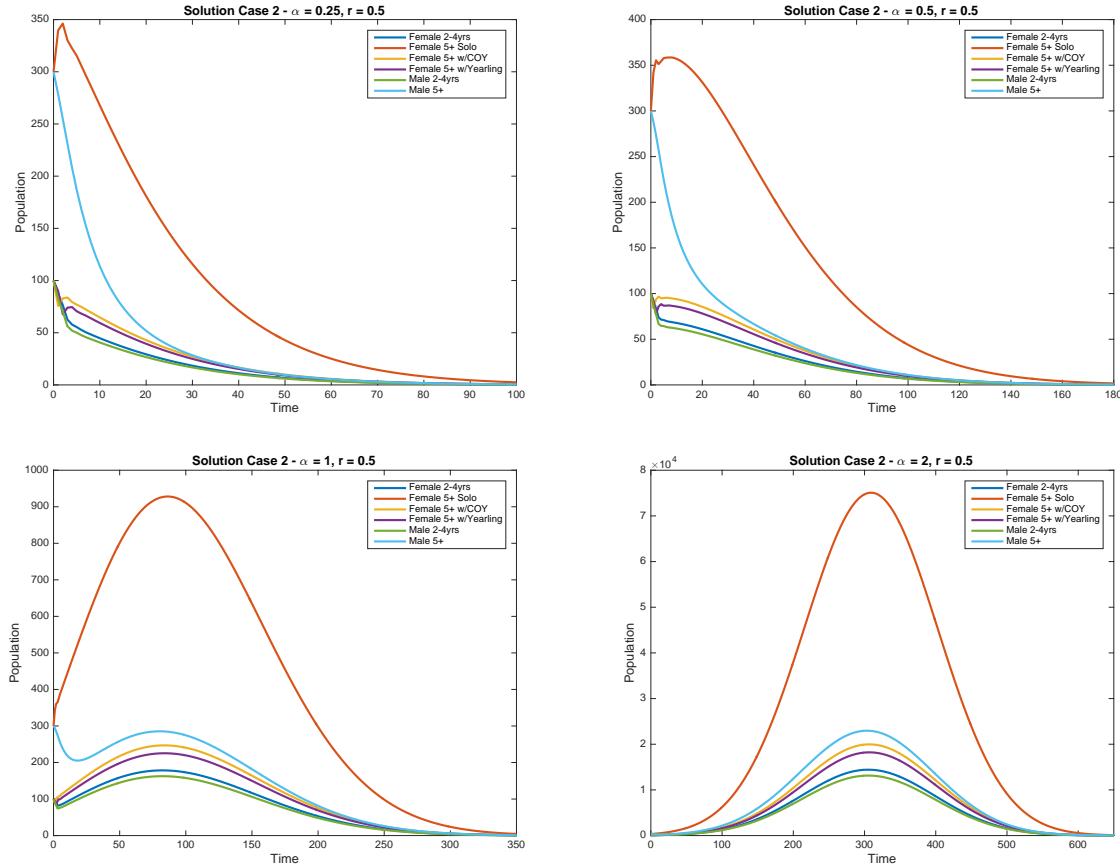


Figure 2.12: Solution curves for Case 2 where both survival and breeding are time-dependent with $k = 0.1$, $r = 0.5$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

Figure 2.13 shows the population curves when α is varying and $r = 1$. For all values of α the population reaches extinction. The population growth reaches a maximum that occurs at different times with the change in α . For $\alpha = 0.25, 0.5, 1$ and 2 the maximum population occurs at approximately 8, 10, 15 and 20 years respectively. The maximum population value occurs at a later time as α increases. When $\alpha = 2$ the population is shown for a maximum of 50 years. This is due to $\sigma_5(t)$ reaching zero at this time.

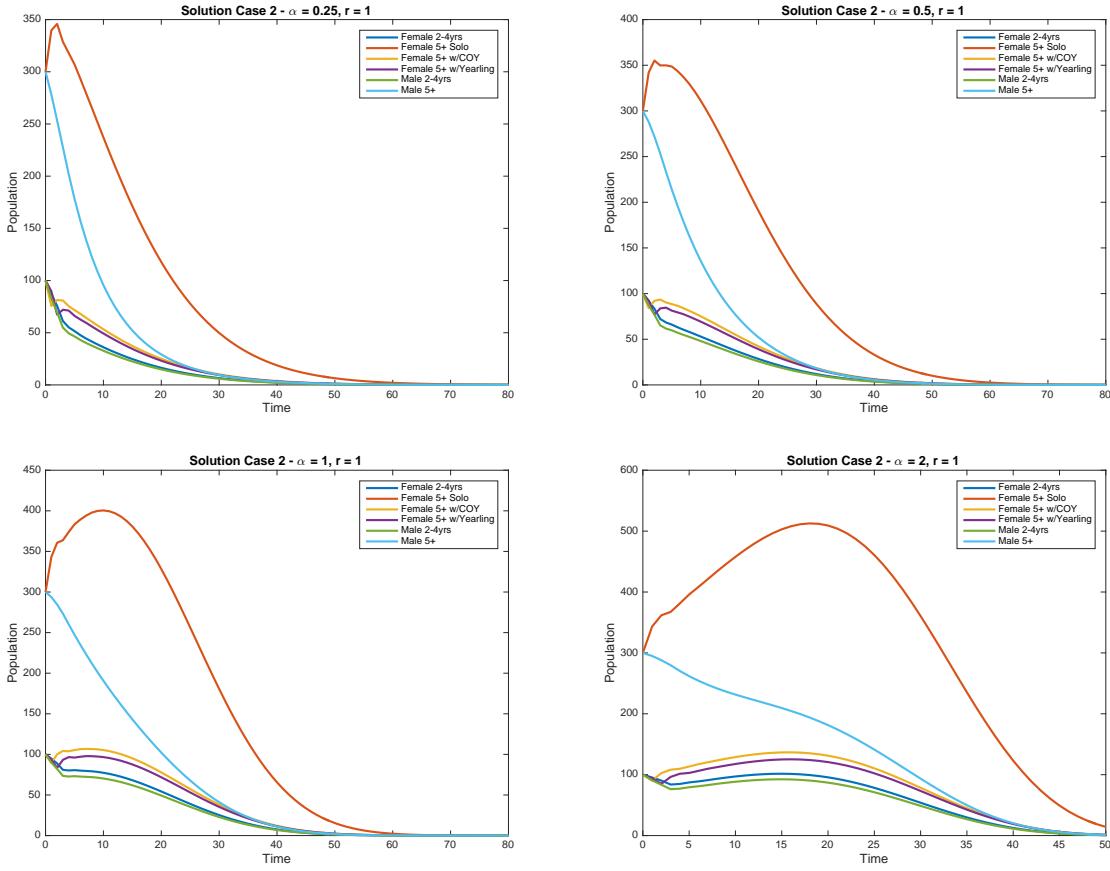


Figure 2.13: Solution curves for Case 2 where both survival and breeding are time-dependent with $k = 0.1$, $r = 1$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

The plots in Figure 2.14 represent when $r = 2$ and α is changing. The time axis in each graph indicates how long the model is valid for. In this case, $\sigma_5(t)$ is the first parameter to reach zero. All values of α result in small population growth followed by large declines. The extinction of the population occurs around 35 years for $\alpha = 0.25$. For all other α values the population is tending towards zero. Once $\sigma_5(t) = 0$ we would expect the population to become extinct.

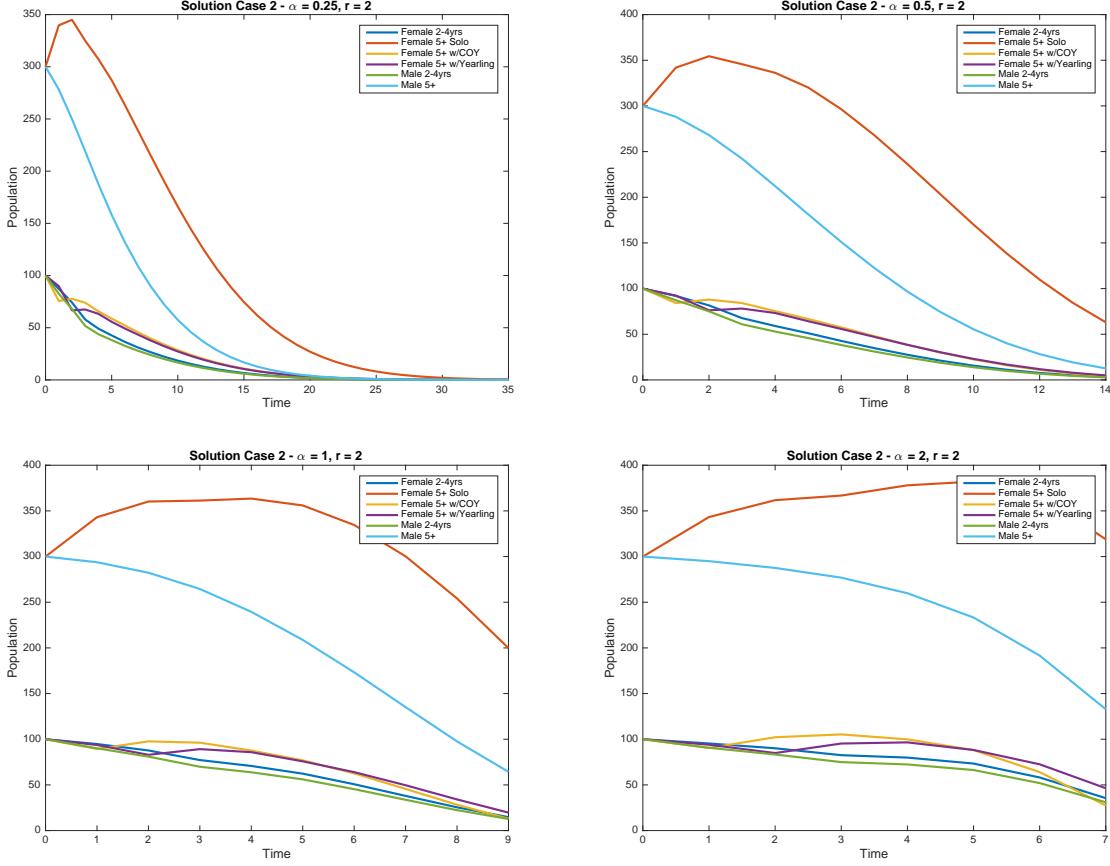


Figure 2.14: Solution curves for Case 2 where both survival and breeding are time-dependent with $k = 0.1$, $r = 2$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

2.5.3 Case 3 - Results

For the third case, the time-dependent parameters were $\sigma_i(t)$, $P_i(t)$ and $\beta_2(t)$. The parameters β_3 and f were left constant, as they were in the previous case. The time-dependent parameters $\sigma_{L1}, \sigma_1, \sigma_5, P_1$ and P_5 took on different values than all other time-dependent parameters. This is due to the fact that juvenile and sub-adult bears are more affected by temperature declines than adult bears. Notice that we did not include σ_{L0} , since COY survival is highly dependent on their mother. We marked the differences in time-dependent parameters by changing the value k . The parameter k took on two different values for this case. For juvenile and sub-adult

stages, the value of k was set as $k = 0.2$ and for all other stages it was set to $k = 0.05$. This allowed the model to simulate the differences between how each compartment is impacted by the temperature change. Initial and constant parameter values were taken from Table 2.2. The parameters a , r and α took on the same values as those used in Case 1 and 2.

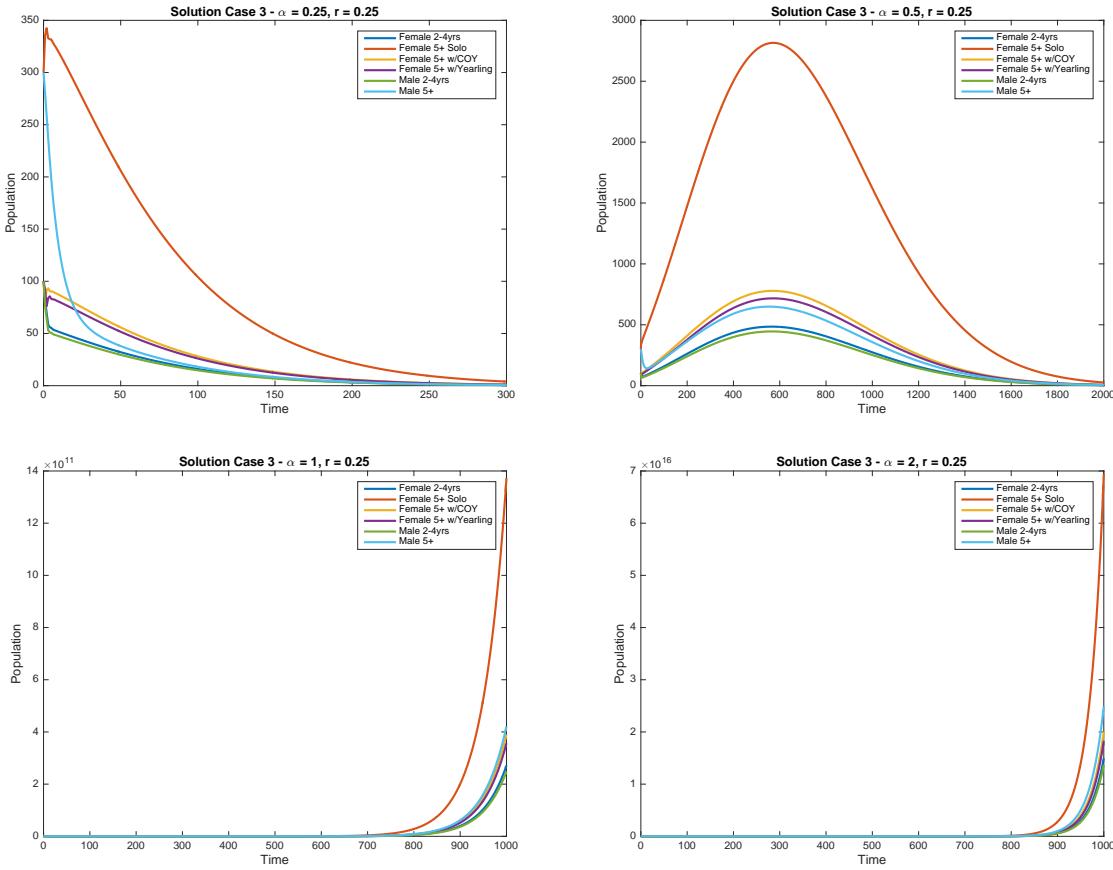


Figure 2.15: Solution curves for Case 3 where both survival and breeding are time-dependent and sub-adult survival is impacted more than other compartments. Here $k = 0.2$ for sub-adult survival and $k = 0.05$ for all other stages, $r = 0.25$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

The solutions are shown in Figures 2.15 - 2.18. The results from the first simulation in case three are displayed in Figure 2.15 when α varies and $r = 0.25$. The population goes to extinction after 300 years when $\alpha = 0.25$ and when $\alpha = 0.5$ the population reaches a peak around

600 years and declines to zero after approximately 2000 years. For both $\alpha = 1$ and $\alpha = 2$ the population growth is exponential for all time.

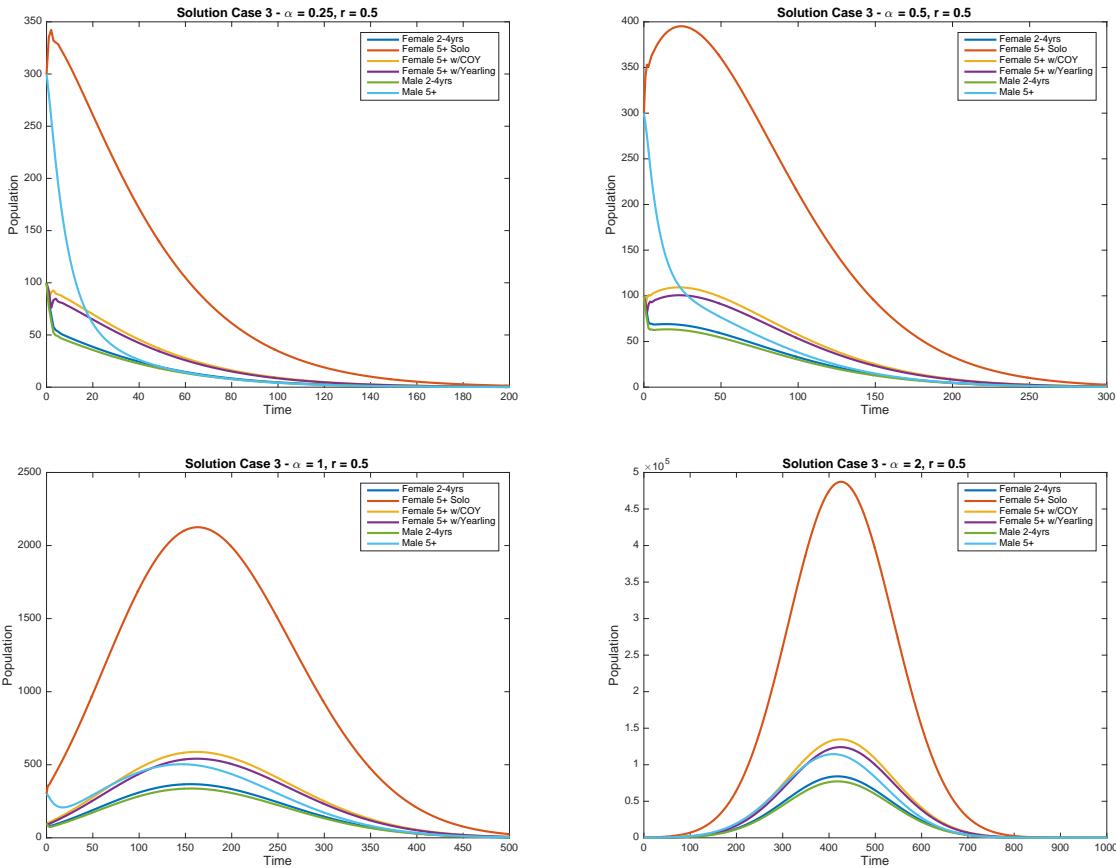


Figure 2.16: Solution curves for Case 3 where both survival and breeding are time-dependent and sub-adult survival is impacted more than other compartments. Here $k = 0.2$ for sub-adult survival and $k = 0.05$ for all other stages, $r = 0.5$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

The solutions shown in Figure 2.16 are for simulations done when $r = 0.5$ and α varied. For all values of α the population reaches a peak and then declines to zero. The peaks of the population shifts to the right with increasing α . The population peaks around 10, 50, 175 and 450 years when $\alpha = 0.25, 0.5, 1$ and 2 respectively. The population reaches extinction level after approximately 200, 300, 500 and 1000 years when $\alpha = 0.25, 0.5, 1$ and 2 respectively.

The females that are 5+ years of age have a population of approximately 450,000 which is not biologically relevant.

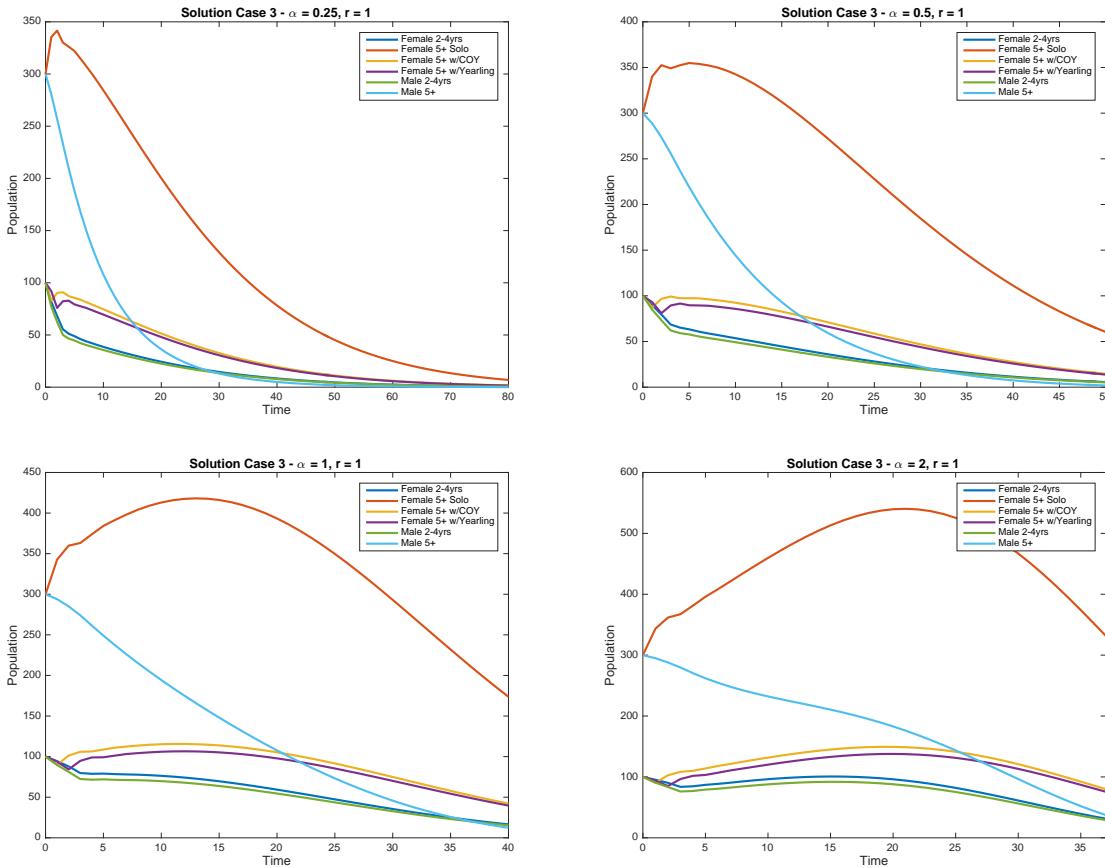


Figure 2.17: Solution curves for Case 3 where both survival and breeding are time-dependent and sub-adult survival is impacted more than other compartments. Here $k = 0.2$ for sub-adult survival and $k = 0.05$ for all other stages, $r = 1$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

Figure 2.17 displays the results of simulations when α is varied and $r = 1$. The results shown are plotted with the maximum time axis possible, after which the model becomes invalid. The population reaches a peak and the peaks shift right with increasing α values. When $\alpha = 0.25, 0.5, 1$ and 2 the population reaches its maximum after 5, 10, 20 and 22 years respectively. The population declines to extinction levels around 80 years when $\alpha = 0.25$. For all

other values of α the population declines are tending towards extinction.

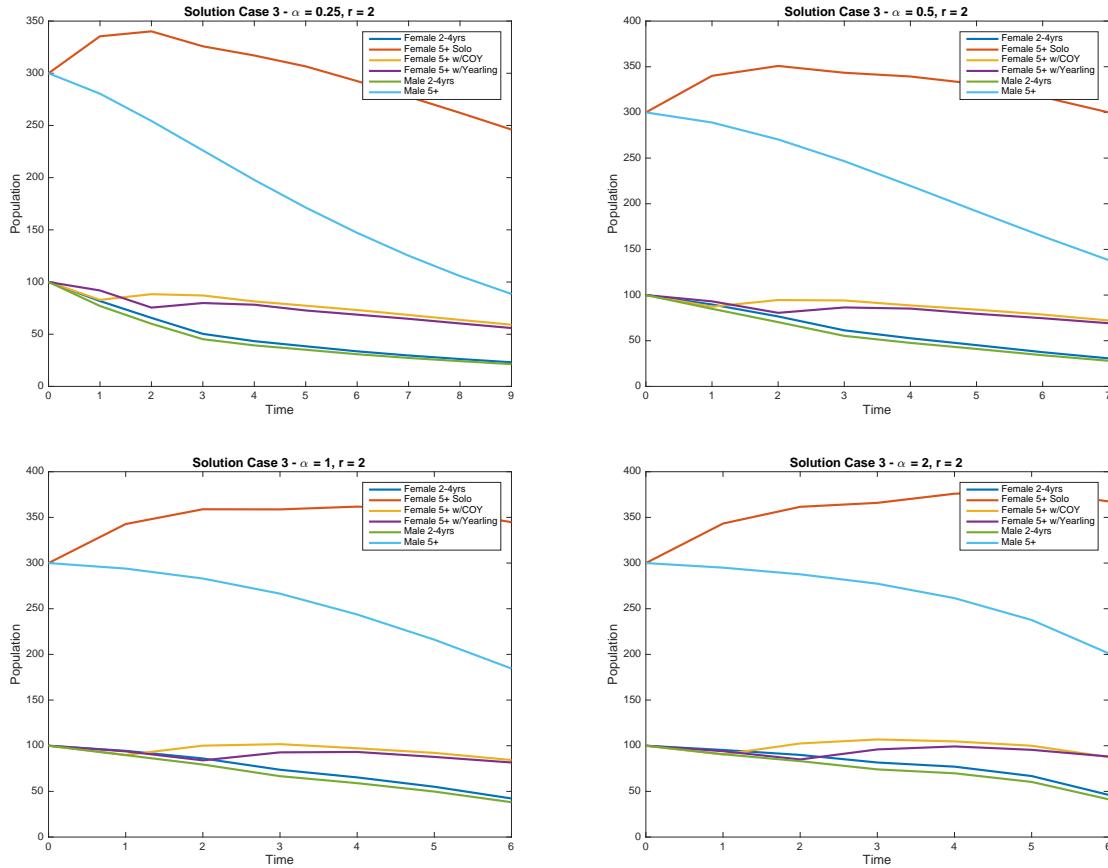


Figure 2.18: Solution curves for Case 3 where both survival and breeding are time-dependent and sub-adult survival is impacted more than other compartments. Here $k = 0.2$ for sub-adult survival and $k = 0.05$ for all other stages, $r = 2$ and α varying. Top left: Solution curves for $\alpha = 0.25$. Top right: Solution curves for $\alpha = 0.5$. Bottom left: Solution curves for $\alpha = 1$. Bottom right: Solution curves for $\alpha = 2$

The last simulation was done using varying α values and $r = 2$. This was the most extreme simulation as the model only remained valid for 9, 7 and 6 years for values of $\alpha = 0.25, 0.5$ and 1 and 2 respectively. The results of the simulation are shown in Figure 2.18. The population declines for all values of α . The declines in the population all appear to be tending towards zero. The parameter $\sigma_5(t)$ is the first to reach zero in this case as well.

2.6 Conclusions and Discussion

The climate changes in the region of WH has been impacting polar bear survival rates and reproduction rates. By creating a time-dependent matrix population model, we were able to construct a model that can represent the polar bear population. Incorporating the increasing temperature as a function that proportionally decreases survival rate and reproduction rates, we were able to predict the future of polar bears under various impact levels. Sensitivity analysis determined the population growth is most sensitive and elastic to changes in the survival probability of breeding females. Furthermore, with less females surviving to breed there will be fewer cubs being born each year.

Incorporating temperature increases into the model was done in three cases: only survival rates are impacted by temperature (Case 1), both survival and breeding are impacted by temperature (Case 2) and both breeding and survival are impacted by temperature, with the impact being greater for younger polar bears (Case 3). Each of the three cases present several scenarios where polar bears reach extinction. There were a few scenarios that resulted in no changes to polar bear population growth. Looking further into each case and the results, we can draw some conclusions about the impact of climate change on polar bears.

When the rate of temperature increase followed a concave down pattern ($r = 0.25$), the temperature increase was rapid for a small time and then slowed down as time increased. For all three cases, the polar bears are unable to survive the temperature increases when the impact of temperature is given by $\alpha = 0.25$ and 0.5 . This indicates that the rapid onset of temperature increases and the impact it has on polar bear survival and breeding is detrimental to polar bears. Polar bears are unable to withstand the sudden impacts of climate change. In Case 2, when the impact of temperature is $\alpha = 0.25$, the extinction time is around 150 years. In Case 1 and 3, it is around 180 and 300 years, respectively. It can be seen that when the climate change impacts both the survival and breeding probabilities, as in Case 2, population declines occur

at the fastest rate and polar bears reach extinction after the shortest amount of time. When $\alpha = 0.5$, the population is able to grow for a period of time before it declines to extinction. The peak in population levels is largest for the last case, when climate change impacts the juvenile and sub-adult bears stronger than the prime-adults. This indicates that polar bears are able to overcome the climate change for a period of time before it passes some threshold and population declines. Extinction does not occur for 1000, 500 and 2000 years for Case 1, 2 and 3. The impact to both breeding and survival in Case 2 causes the quickest extinction because the impact to breeding is limiting the population growth. When $\alpha = 1$ and 2, the impact of temperature is slow to begin and rapid as time increases. For all three cases, the polar bears are able to overcome the onset of temperature, since the impacts on their survival and breeding do not occur until later in time when the increases in temperature are slower. The population growth then remains exponential, which is unrealistic. Including density-dependence into the model will prevent exponential growth.

If the temperature increase was to follow a different concave down pattern ($r = 0.5$), the increases would occur quicker and take longer to slow down than when $r = 0.25$. The rate of increase would be slower than when $r = 0.25$. In all three cases the polar bears are unable to survive the changing climate. The population reaches extinction level for each α value. Similar to the previous discussion when $r = 0.25$, we can see that declines occur fastest when the impact of temperature is given by $\alpha = 0.25$. For Case 2, the polar bear population goes extinct after 100 years. This implies the impact to both breeding and survival probabilities is too much for the polar bears to overcome. For both $\alpha = 0.5$ and 1 in all three cases, the population is able to grow before it hits some threshold and starts declining rapidly. When the impact of temperature is equal to the increase in temperature or slightly larger, the polar bear growth is not limited by temperature until it reaches some critical time. This critical time marks the smallest survival and breeding probabilities that allow population growth. Once climate change causes the survival and breeding probabilities to decrease beyond this level, the population reaches ex-

tinction. Lastly, when $\alpha = 2$ the population exhibits the same behaviour as $\alpha = 0.5$ and $\alpha = 1$. However, the peak in population reaches unrealistic levels. The population exceeds 170,000 bears for Case 1, 80,000 bears for Case 2 and 500,000 bears for Case 3. These populations are not biologically relevant, so we assume the population growth will be exponential here. If we incorporated density dependent survival and breeding probabilities here, we would not be able to reach these high population levels.

The temperature increases demonstrated by the region of WH have been linear thus far. Therefore, when $r = 1$ we want to examine the results further as they can indicate current trends in the population dynamics. In all three cases, the polar bear population reaches zero. The steepness of the population declines depend on the impact of temperature change. For Case 1 and 2, when $\alpha = 0.25, 0.5$ and 1 the larger the impact, the steeper the decline. The polar bears are going extinct after 80 years for all impact levels. With increasing α the population is able to grow for a period of time before it declines rapidly. The length of time before the population begins to decline also increases with the impact. For both Case 1 and 2, the population levels peak around 8, 10 and 15 years for $\alpha = 0.25, 0.5$ and 1 . The peak in population is occurring later for larger α since for small values of time the smaller impact will dominate. The maximum population peak occurs when $\alpha = 1$ for both cases 1 and 2 where the population is around 1000 bears. This critical time at which the population peaks will mark the smallest survival and breeding probabilities that allow population growth. Once climate change causes the survival and breeding probabilities to decrease beyond this level, the polar bears will go extinct. For all of Case 3 and when $\alpha = 2$ in Case 1 and 2, the population trends are all indicating that extinction will occur. The survival probability of sub-adult males, $\sigma_5(t)$, reaches zero before the population does. When this occurs, the model is no longer valid as probabilities cannot be less than zero. The parameter $\sigma_5(t)$ reaches zero first because it is the smallest value initially. Once this happens, we know the other parameters will be soon to follow. In Case 3 in particular, without the juveniles and sub-adults surviving to reproduction age, the population

will collapse. The population could reach extinction in 50 years based on the scenarios displayed by Case 3.

If the rate of temperature increase was to follow a concave up pattern ($r = 2$), the increases in temperature would be small for smaller values of time and increases would be large for bigger values of time. When the impact of temperature increased, the amount of time the model remained valid decreased. The probability $\sigma_5(t)$ reached zero after 35, 14, 9 and 7 years for both Case 1 and 2 for $\alpha = 0.25, 0.5, 1$ and 2 respectively. It reached zero after 9, 7, 6 and 6 years for Case 3 when $\alpha = 0.25, 0.5, 1$ and 2 . For Case 3, this indicates that sub-adult males cannot withstand the impact of climate change for more than a decade. The population trend is negative once the model becomes invalid, so we would assume that the population would continue this trend and polar bears would reach extinction. For Case 1 and 2, the population trends follow the same pattern for each α . The population also declines to extinction for each. When the rate of temperature increase is quadratic, it has the most extreme impact on the population.

The overall trends displayed by Case 1 and Case 2 are similar for all values of r and α . The only difference observed between these cases is the overall population values in Case 1 are higher than those in Case 2. When only survival probabilities are impacted by the increasing temperatures as in Case 1, the population values are larger. The population values are smaller for Case 2, due to having both the survival and breeding probabilities impacted by climate change. We can see that when breeding is effected by the increases in temperature, the population levels are smaller and it reaches extinction faster than when breeding is not effected.

Regehr et al. demonstrated that juvenile and sub-adult bears are more affected by climate change than prime-adults [14]. Case 3 was representative of this result as temperature increases had a larger impact on survival probabilities of juveniles and sub-adults. Overall, the population tended to zero for most values of α and r . When $r = 0.25$ and $\alpha = 1$ and 2 the population

growth remained exponential. All other values resulted in the population going extinct. The amount to time it takes for polar bears to go extinct decreased with increasing r and increased with increasing α . When $r = 1$, the current increasing temperature trend is exhibited and Case 3 exhibits the current impact on each compartment of the population.

In conclusion, we can expect that the population of polar bears in Western Hudson Bay will not overcome the changes in temperature. The longest amount of time predicts the population will reach extinction after 300 years. However, the shortest amount of time predicted polar bear populations will reach extinction after 6 years in the extreme case. Currently, the trend of temperature increase is linear so we should expect the population will follow the trend observed by Case 3 when $r = 1$. Therefore, if the impact of global warming is to demonstrate the trends displayed here, the polar bears in western Hudson Bay will be extinct within the next 50 -80 years.

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Chapter 3

Delay Differential Equations with Time-Dependent Parameters

3.1 Introduction

Polar bears are marine mammals that live in the Arctic [15]. They are highly dependent on ice for all major aspects of life which include hunting, mating and travelling [12, 11, 24]. The dependence on the ice is important to understand because in the Arctic and Western Hudson Bay (WH) in particular, the polar bears have been experiencing the effects of climate change [16, 23, 24]. The increases in the air temperature have resulted in earlier sea-ice break up and a longer ice-free season [17, 18]. As a result, several researchers are seeing changes in body condition, survival and reproduction rates for polar bears in this region [20, 14, 1, 18, 23]. Other regions in the southern Arctic are also being impacted by global warming, however the focus for this model is for the Western Hudson Bay population.

Most modelling approaches used for polar bears have been discrete matrix populations models, both stochastic and demographic [9, 8, 18, 12]. Matrix population models are able to determine the long term population growth rates and estimate the stable stage distribution of

the population [2]. The models used for polar bears look at discrete time, however, we believe that it will be of better interest to create a model with continuous time. This will allow us to see the short term dynamics that occur within each year, such as mating, rather than considering the year as a whole.

Molnár et al. created a system of ordinary differential equations (ODEs) to model the mating dynamics of polar bears [13]. Their model was used to find the presence of the Allee effect. The Allee effect is described by a relationship between the population density and mean fitness, such as the population growth rate [4]. Populations that exist in low densities, such as polar bears, are vulnerable to these effects because of the low frequency of mating encounters [13]. It is important to understand what could cause Allee effects because they can accelerate declines in population and possibly lead to extinction. With their model, Molnár et al. were able to identify that the Allee effect for polar bears is dependent on the operational sex ratio which is given by the density of males over the density of females [13]. They also determined that mating success was a strong non-linear function of the sex ratio. Thus, when mating success starts declining due to decreases in male density a small additional loss of males could cause reproductive collapse [13]. The sex ratio was also a function of the overall density of polar bears. Furthermore, as the overall density decreases an increase in male density is required to maintain the mating success rate. Additionally, they found that mating success was most sensitive to the changes in the pair formation rate especially at low densities.

The presence of Allee effects indicates that polar bears are highly susceptible to rapid population declines. Polar bears already exist at low densities and reproduction rates are small so it is important to understand how the population will respond under climate change [13, 24]. The warming air temperatures are impacting polar bear survival and could result in an even lower density of polar bears [24]. Additionally, a lower density can effect the males' ability to locate females during the mating season and impact the reproduction rate. Since males track females

during mating season using tracks on the sea-ice [13], without the presence of sea-ice tracking females will be harder. Changes in the survival rates of both males and females could result in changes in the sex ratio. Moreover, changes in the sex ratio could cause a severe population decline and possible extinction.

We wanted to extend the framework provided by Molnár et al. to include the dynamics of polar bears outside the mating season [13]. We aimed to develop a system of delay differential equations (DDEs) that can represent the polar bear population density throughout the season. By incorporating these yearly dynamics, we are also able to construct a framework that allows us to research the impact of climate change. Incorporating temperature increases affecting death and survival rates, we can predict how the population will behave under various temperature impact levels. In our model, we do not assume any density dependence so we will not have any Allee effects. However, the framework of our model will allow for the incorporation of density dependent mechanisms and may be of interest for future work.

3.2 The Development of the Model

A system of DDEs was created by incorporating the yearly dynamics of polar bears, such as deaths and births, into the mating system model in Molnár et al [13]. The framework provided by them allowed us to incorporate the birth of new cubs as a result of mating success.

3.2.1 The Dynamics of Polar Bears

The mating season for polar bears is believed to be from early March to early June [13, 24]. A peak in mating usually occurs around April to early May [13]. The amount of time females and males stay paired during the mating season depends on the females oestrus period which can last up to 4 weeks [13]. Male polar bears 4-5 years of age are considered sexually mature

and available for mating [13]. During the mating season, males search for females by following their tracks [13]. This searching can be demanding and males will often sacrifice hunting during this time [13]. Once males separate from females they have the ability to continue mate searching until the end of the mating period or they can stop mate searching [13]. Furthermore, polar bears are polygynous since males can mate with more than one female if time permits [13].

Female polar bears 4-5 years of age are considered sexually mature and available for mating. After males pair with females during the mating season they may become pregnant. Pregnant females will carry cubs for 8 months before giving birth to cubs of the year (COY) [24, 14, 1]. Once cubs are born, they remain with their mother for 2 years [9, 11, 24, 8]. The survival of cubs is highly dependent on the survival of their mother during the first 2 years [9, 19]. Once cubs are weaned they are responsible for their own survival [10]. The mothers of weaned bears also become available for breeding again [24].

3.2.2 The Model

We modelled the pairing dynamics of polar bears based on the model of Molnár et al. by explicitly incorporating a pair formation rate σ , a separation rate, μ , and the ability of males to continue mate searching, α [13]. We assumed that mature males and females are able to mate when they are of maturation age of 4 years. For mature females we also include mothers with 2 year old cubs as available for breeding. We let $M(t)$ and $F(t)$ represent the density of the mature solitary males and females, respectively. Males and females form pairs during the mating season at rate σ and separate at rate μ resulting in a sub-population consisting of paired bears denoted by $2P(t)$. The portion of males that continue to mate search within the season is given as α and the portion of males that stop mate searching is given by $(1 - \alpha)$. The density of males that do not continue mate searching are represented by $M^*(t)$. The portion of females

that become pregnant by the end of the mating season is given by β and the portion that are unsuccessful as $(1 - \beta)$. Pregnant female density is represented by $F^*(t)$. Females with COY and yearlings are included among the pregnant females. Females return to mating after 2 years, τ_1 , which is dependent on their survival. The cubs that survive to 4 years, τ_2 , move into the male and female mating sub-population. We assumed the birth of new cubs is a result of successful pairs from 4 years ago. We also assume that successfully pregnant females have 2 cubs, one male and one female whose survival depends on the mother for the first two years. The survival of the mother and cub units is denoted by S_4 . When the cubs are weaned their survival of the immature period (age 2 to 4) is given by, S_1 and S_2 which is now dependent on their sex. We assume that each sub-population of bears has a death rate, d_1, d_2, d_3 and d_4 , except for the bears that are paired. Since pairing only occurs for a short period of time, we can assume all bears survive this period.

Since the model is considering the whole year rather than just mating season we need σ to be a function of time $\sigma(t)$. This allows us to have the pair formation rate turn on during the mating season and off for the remainder of the year. We let t_m be the length of the mating season and δ the mating season residual. This residual ensures that the onset of pair formations will occur slowly and the separation at the end of the mating season will also gradually decrease rather than having it start and end abruptly. Similarly, we let the death rates d_i be functions of time whose explicit form will be discussed in Section 3.2.3. By doing so, this allows us to incorporate how temperature changes with time and impacts the death rates of polar bears.

The system of DDEs that represent these dynamics is given as,

$$\begin{aligned}
\frac{dM}{dt} &= -\sigma(t)MF - d_1(t)M + \alpha\mu P + \beta\mu S_1(t)P(t - \tau_2) \\
\frac{dF}{dt} &= -\sigma(t)MF - d_2(t)F + (1 - \beta)\mu P + \beta\mu S_4(t)P(t - \tau_1) + \beta\mu S_2(t)P(t - \tau_2) \\
\frac{dP}{dt} &= \sigma(t)MF - \mu P \\
\frac{dM^*}{dt} &= (1 - \alpha)\mu P - d_3(t)M^*(t) \\
\frac{dF^*}{dt} &= \beta\mu P - d_4(t)F^* - \beta\mu S_4(t)P(t - \tau_1),
\end{aligned} \tag{3.1}$$

where

$$\sigma(t) = \begin{cases} \sigma_0 & \text{if } 0 \leq t \leq t_m \\ -\frac{\sigma_0}{\delta}t + \sigma_0(1 + \frac{t_m}{\delta}) & \text{if } t_m < t \leq T_m + \delta \\ 0 & \text{if } t_m + \delta < t \leq 1 - \delta \\ \frac{\sigma_0}{\delta}t + \sigma_0(1 - \frac{1}{\delta}) & \text{if } 1 - \delta < t \leq 1 \end{cases} \tag{3.2}$$

$$S_1(t) = \exp\left(-\int_{t-\tau_2}^{t-\tau_1} d_4(s)ds\right) \exp\left(-\int_{t-\tau_1}^t d_1(s)ds\right) \tag{3.3}$$

$$S_2(t) = \exp\left(-\int_{t-\tau_2}^{t-\tau_1} d_4(s)ds\right) \exp\left(-\int_{t-\tau_1}^t d_2(s)ds\right) \tag{3.4}$$

$$S_4(t) = \exp\left(-\int_{t-\tau_1}^t d_4(s)ds\right). \tag{3.5}$$

Parameter	Definition
$M(t)$	Density of solo males of mating age
$F(t)$	Density of solo females of mating age
$P(t)$	Density of pairs of mating males and females
$M^*(t)$	Density of solo males that stop mating during the mating season
$F^*(t)$	Density of pregnant females and females with COY and yearlings
$\sigma(t)$	Pair formation rate
σ_0	Constant pair formation rate, during mating season
μ	Pair separation rate
α	Male re-mating ability
β	Breeding success rate
$d_1(t)$	Male death rate
$d_2(t)$	Female death rate
$d_3(t)$	Non-mating male death rate
$d_4(t)$	Pregnant female and mother/cub death rate
$S_1(t)$	Immature male survival rate
$S_2(t)$	Immature female survival rate
$S_4(t)$	Pregnant female survival rate
τ_1	Pregnancy and weaning period of females bears
τ_2	The length of the immature period from cub to reproduction age
t_m	Length of mating season
δ	Mating time residual
$T(t)$	Function of the average daily temperature
T_0	Average daily temperature
a	Average daily increase in temperature
Δ_0	Magnitude of daily temperature fluctuations
A	Shift in period
d_i^*	Death rate at ideal temperature
T^*	Ideal daily temperature

Table 3.1: Descriptions of all parameters used in the model

3.2.3 Time-Dependent Death Rate

The death rates for polar bears can normally be assumed constant, however the aim of this work is to look at how increasing air temperatures will impact polar bear survival which implies that death rates are not constant. For simplicity, we assumed that only death rates and survival rates would be affected by the temperature increases. Thus, we created a function for the death rates that was an increasing function of temperature. First, we defined the average daily temperature

as,

$$T(t) = \left[(T_0 + at) + \Delta_0 \sin\left(\frac{2\pi(t+A)}{365}\right) \right] \quad (3.6)$$

where a is average daily temperature increase, T_0 the average daily temperature, Δ_0 the magnitude of temperature fluctuations and A the shift in period. We set T^* as the maximum ideal temperature for polar bears. When temperatures are below T^* the death rate remains as a constant, d_i^* which are the death rates before temperature change. When temperatures are above T^* the death rate will increase as a function of $T(t)$. With a simple linear increasing equation the death rate can be given as,

$$d_i(t) = d_i^* + k \max(0, (T(t) - T^*)) \quad (3.7)$$

where k is the proportionality constant that measures the increases in death rate in units of bears per degree. A summary of all unknowns and parameters used in the system along with their description are shown in Table 3.1.

3.3 Positivity of Model and Initial Conditions

First, we note that the last two equations in (3.1) are actually decoupled from the first three. Thus, we only need to analyse the subsystem consisting of the first three equations,

$$\begin{aligned} \frac{dM}{dt} &= -\sigma(t)MF - d_1(t)M + \alpha\mu P + \beta\mu S_1(t)P(t - \tau_2) \\ \frac{dF}{dt} &= -\sigma(t)MF - d_2(t)F + (1 - \beta)\mu P + \beta\mu S_4(t)P(t - \tau_1) + \beta\mu S_2(t)P(t - \tau_2) \\ \frac{dP}{dt} &= \sigma(t)MF - \mu P. \end{aligned} \quad (3.8)$$

Once we have known the dynamics of $M(t)$, $F(t)$ and $P(t)$ from (3.8), the behaviour of $M^*(t)$ and $F^*(t)$ are fully determined by the last two equations in (3.1), or alternatively by

$$\begin{aligned} M^*(t) &= M^*(0) \exp \left(\int_0^t d_3(s) ds \right) + \int_0^t (1 - \alpha) \mu P(s) \exp \left(\int_s^t d_3(\xi) d\xi \right) ds \\ F^*(t) &= \int_{t-\tau_1}^t \beta \mu P(s) \exp \left(\int_s^t d_4(\xi) d\xi \right) ds \end{aligned} . \quad (3.9)$$

We first address the positivity of solutions to (3.8) with given positive initial conditions. To this end we need to use the following Theorem from Smith [21], which establishes the positivity of a general DDE system of the form

$$\begin{aligned} \dot{x}(t) &= f(t, x_t) \quad t > 0 \quad x \in \mathbb{R}^n \\ x(\theta) &= \phi(\theta) \quad \text{for } \theta \in [-\tau, 0] \end{aligned} . \quad (3.10)$$

Theorem 3.1 (Smith, [21]) - Assume whenever $\phi \in D$ satisfies $\phi \geq 0$, $\phi_i(0) = 0$ for some i and $t \in \mathbb{R}$, then $f_i(t, \phi) \geq 0$. If $\phi \in D$ satisfies $\phi \geq 0$ and $t_0 \in \mathbb{R}$, then $x(t, t_0, \phi) \geq 0$ for all $t \geq t_0$ in its maximal interval of existence.

Applying the abstract notation of Theorem 3.1 to the system of DDEs given in (3.8), we have $x_1 = M$, $x_2 = F$ and $x_3 = P$ and

$$\begin{aligned} f_1(t, \phi) &= -\sigma(t)\phi_1(0)\phi_2(0) + \alpha\mu\phi_3(0) - d_1(t)\phi_1(0) + \beta\mu S_1(t)\phi_3(-\tau_2) \\ f_2(t, \phi) &= -\sigma(t)\phi_1(0)x_2(0) - d_2(t)\phi_1(0) + (1 - \beta)\mu\phi_3(0) + \beta\mu S_4\phi_3(-\tau_1) + \beta\mu S_2(t)\phi_3(-\tau_2) \\ f_3(t, \phi) &= \sigma(t)\phi_1\phi_2 - \mu\phi_3 \end{aligned} . \quad (3.11)$$

we determine the system remains positive on its maximum level of existence if the initial conditions are positive. If we choose the initial conditions of the DDEs to be positive then we can actually know that the solution remains positive.

The initial conditions for the system cannot all be given as constants. Referring to Gourley and Zou [5], initial data can be provided using a compatibility condition for which initial data is not arbitrary but depends on other initial data. Moreover, for the system (3.9) the density of pregnant females is not arbitrary, rather it is a result of the successful pairs from the previous

two years. Utilizing the compatibility condition the initial conditions for (3.1) has the form,

$$\begin{aligned}
 M(t) &= M_0 \geq 0 & t \in [-\tau_1 - \tau_2, 0] \\
 F(t) &= F_0 \geq 0 & t \in [-\tau_1 - \tau_2, 0] \\
 M^*(t) &= 0 & t \in [-\tau_1 - \tau_2, 0] \\
 P(t) &= \sigma(t)M_0F_0 & t \in [-\tau_1 - \tau_2, 0] \\
 F^*(t) &= \int_{-\tau_1}^0 \beta \mu P(s) \exp\left(-\int_s^0 d_4(\xi) d\xi\right) ds & t \in [-\tau_1, 0].
 \end{aligned} \tag{3.12}$$

3.4 Numerical Simulations

3.4.1 Parameter Estimations

We choose the initial time ($t = 0$) as March 1st to be the start of the mating season. Thus, one full year is from March until the following March. We also choose to have all model parameters to be in terms of days, so we will be able to see what is happening in the model more clearly. The average mating time is taken from Molnár et al. to be 60 days [13]. The residual mating season, δ , is taken as 5 days. We assume, the WH population will have the same pair formation and separation rates as the Lancaster Sound population as calculated by Molnár et al. [13]. For simplicity, we let the male mating ability $\alpha = 1$. The portion of females that successfully breed during mating season is taken as $\beta = 0.31$ [12]. The ideal death rates for each class of polar bears can be estimated as the reciprocal of their life expectancy. For male polar bears life expectancy is 25 years and for females it is 30 years [6].

The air temperatures in WH were estimated by using the average monthly temperatures in Churchill, Manitoba. This city is central to this region as illustrated in Figure 3.2 and the density of polar bears is largest in this area [22]. Therefore, it will provide a good approximation for temperatures of the region. Temperature data was found and it allows us to estimate most parameters in Equation 3.6 [3]. We assume the average monthly temperatures will occur on the

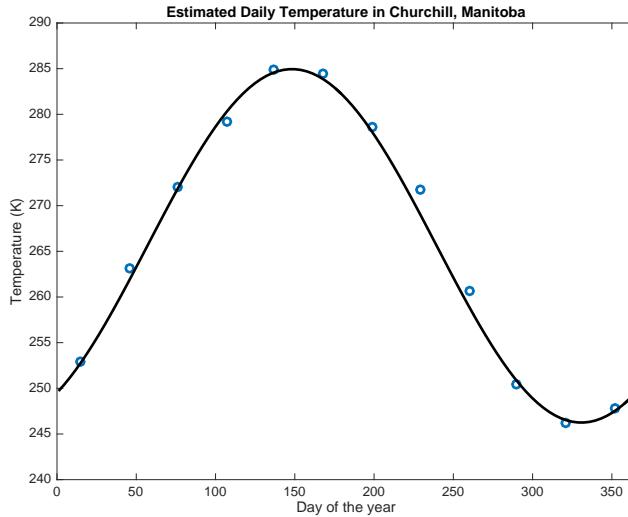


Figure 3.1: The daily average temperature in Churchill, Manitoba. The solid line is the estimated function $T(t) = T_0 + \Delta_0 \sin\left(\frac{2\pi(t+A)}{365}\right)$ fitted to the data and the open circles are the data points from Table 3.2.

15th day of each month. The temperatures are converted to Kelvin (K) in order to avoid the use of negative values. The data in Table 3.2 is fit using the equation $T(t) = T_0 + \Delta_0 \sin\left(\frac{2\pi(t+A)}{365}\right)$, from (3.6) but ignoring the average temperature increase, a . The results of the interpolation are shown in Figure 3.1. The average temperature a is estimated using the information provided by Stirling et al. that the average increase in air temperatures was $2 - 3^\circ\text{C}/\text{decade}$ in WH [23]. The ideal temperature was taken as the average temperature in Churchill, which is -11°C [3].

Month	Temperature ($^{\circ}\text{C}$)	Temperature (K)
January	-26.9	246.25
February	-25.4	247.75
March	-20.2	252.95
April	-10	263.15
May	-1.1	272.05
June	6.1	279.25
July	11.8	284.95
August	11.3	284.45
September	5.5	278.65
October	-1.4	271.75
November	-12.5	260.65
December	-22.7	250.45

Table 3.2: Average monthly temperature in Churchill, Manitoba.

We were unable to locate specific data about the density of each subclass of polar bears. Instead, the population estimates for males and females of reproduction age are taken from Chapter 2 to be 300 males and 300 females. Figure 3.2 illustrates the boundaries of the WH region. Stapleton et al. approximated this area to be 435,000 km² [22]. Upon calculation, the initial densities of solo males and solo females can be determined. Since the model is beginning at the start of the mating period, the initial density of pairs and non-mating males is taken to be zero. The pregnant female density is calculated using the equation from the initial conditions (3.12). A summary of all parameter values along with their units are provided in Table 3.3.



Figure 3.2: A map illustrating the region of Western Hudson Bay. The star is the city of Churchill, Manitoba. Modified version of map provided by the IUCN Polar Bear Specialist Group [7].

Parameter	Value	Units
α	1	-
β	0.31	-
μ	$\frac{1}{17.5}$	days ⁻¹
σ_0	49.2	km ² per day
t_m	60	days
δ	5	days
τ_1	730	days
τ_2	1460	days
d_1^*	1.0959×10^{-4}	bears per day
d_2^*	9.1324×10^{-5}	bears per day
d_3^*	1.0959×10^{-4}	bears per day
d_4^*	9.1324×10^{-5}	bears per day
T_0	262.15	K
Δ_0	19.35	-
A	308	-
a	$\frac{0.03}{365}$	K per day
T^*	268.15	K
M_0	6.89×10^{-4}	bears per km ²
F_0	6.89×10^{-4}	bears per km ²
P_0	0	bears per km ²
M_0^*	0	bears per km ²
F_0^*	5.14×10^{-5}	bears per km ²
k	0 to 5×10^{-4}	bears per degree

Table 3.3: All parameter values and units used for the DDE. Unitless parameters are denoted by ‘-’.

3.4.2 Results

The system of DDEs (3.1) presents many difficulties for analytic analysis due to the complexities of the time-dependent parameters. Consequently, a numerical approach is required to solve the system. Simulations are done using a DDE solver in MATLAB. The proportionality constant k in (3.7) was varied to investigate how the impact of temperature would affect the population numbers.

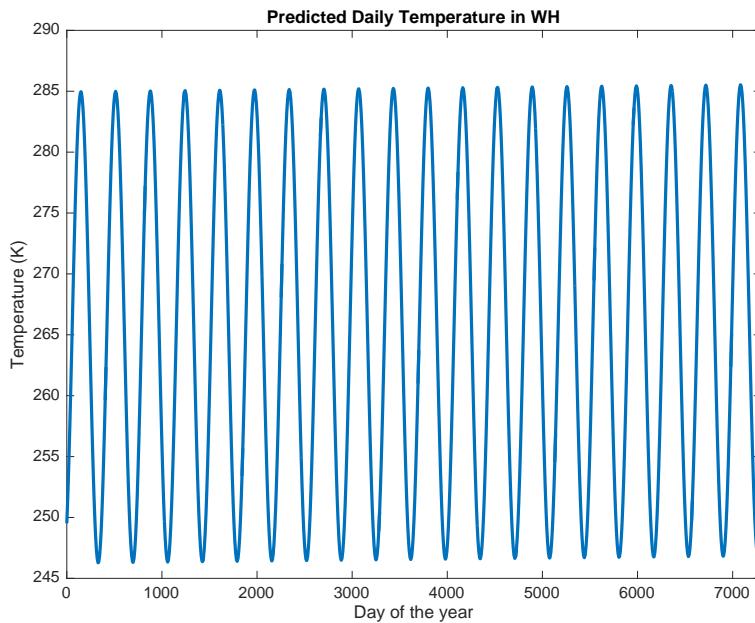


Figure 3.3: The predicted temperatures for western Hudson Bay over the next 20 years.

The predicted temperature for WH over the next 20 years with increases of 3°C per decade is shown in Figure 3.3. By setting $k = 0$, the solution curves will represent the population of polar bears when temperature is not increasing shown in Figure 3.5. Figures 3.4 and 3.5 display how the population grows without the warming climate. Figure 3.4 displays the population after 1 year to see clearly how the mating system works within the population. The paired and pregnant female population increases as male and female sub-populations decrease during the mating season.

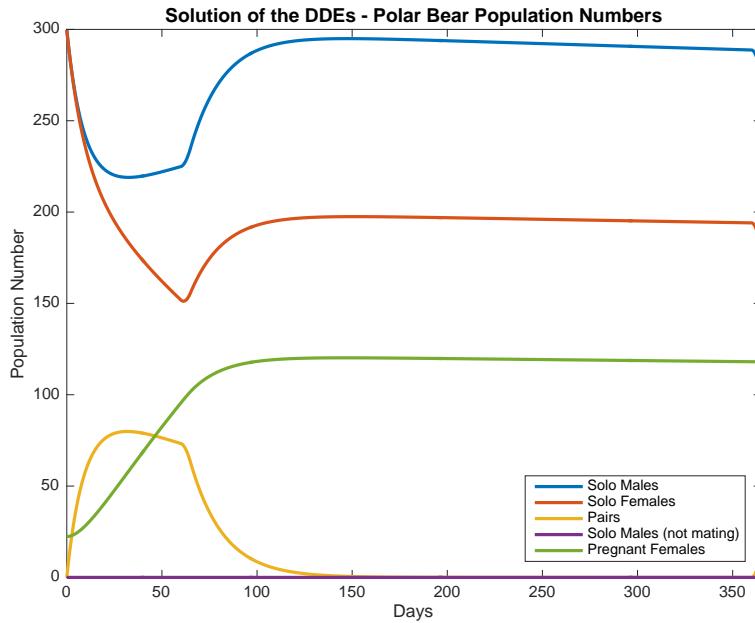


Figure 3.4: The solution to the system of DDEs after 1 year. This figure highlights the features of the mating system of polar bears.

Simulations are done for k values varying from 1×10^{-8} to 5×10^{-4} and results are displayed in Figures 3.6 to 3.13. The "bumps" in the solution curves represent one year and are a result of the mating system. When $k = 1 \times 10^{-8}$, the impact of climate is relatively small and Figure 3.6 shows the population growth is exponential. Population growth is also exponential when $k = 1 \times 10^{-5}$ as shown in Figure 3.7. Increasing to $k = 4.7 \times 10^{-5}$, the population declines for a short period of time before continually increasing. This is shown in Figure 3.8. When $k = 4.8 \times 10^{-5}$ the population declines quadratically and reaches extinction after 150+ years as displayed by Figure 3.9

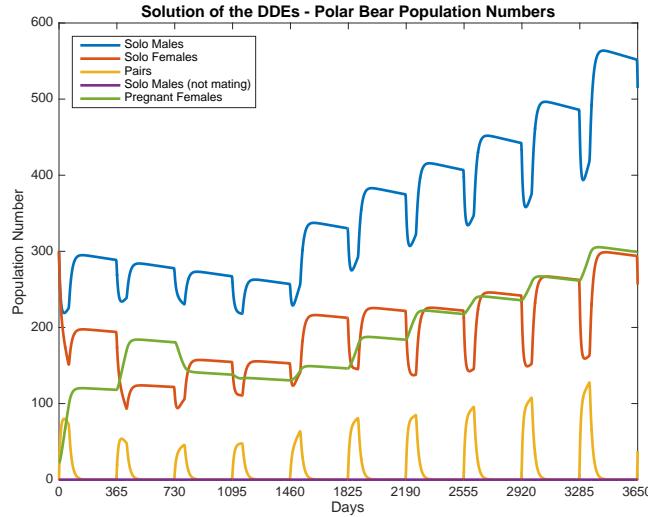


Figure 3.5: The solution to the system of DDEs (3.1) when $k = 0$. This represents when climate change is not included.

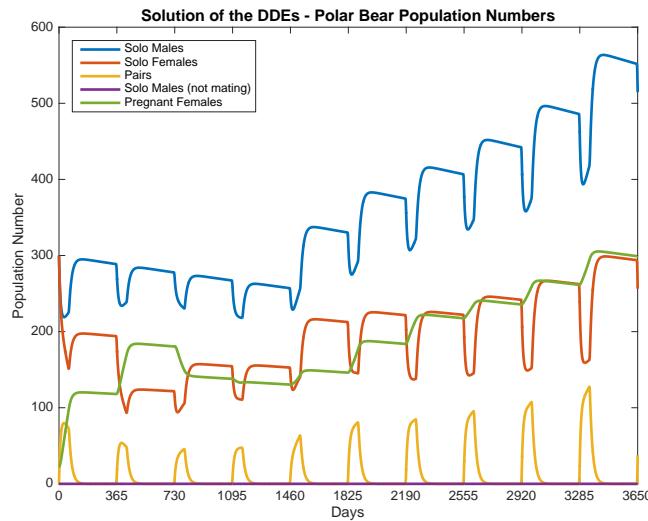


Figure 3.6: The solution to the system of DDEs (3.1) when the impact of temperature is relatively small $k = 1 \times 10^{-8}$.

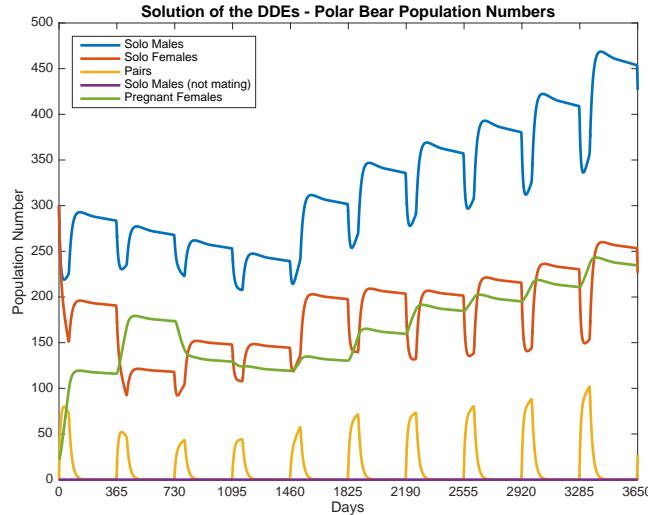


Figure 3.7: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 1 \times 10^{-5}$.

When the impact of climate warming reaches $k = 5 \times 10^{-5}$ the population begins to decline quadratically as well. Figure 3.10 shows the population numbers reach extinction after 100+ years. For $k = 8 \times 10^{-5}$ the population numbers decrease exponentially. The numbers reach extinction after approximately 50 years as displayed in Figure 3.11. When the impact of climate warming is larger, $k = 1 \times 10^{-4}$, the population numbers reach extinction after 25 years. This case can be seen in Figure 3.12. Lastly, when k is increased to $k = 5 \times 10^{-4}$ the population rapidly declines and reaches extinction after 5 years as displayed in Figure 3.13

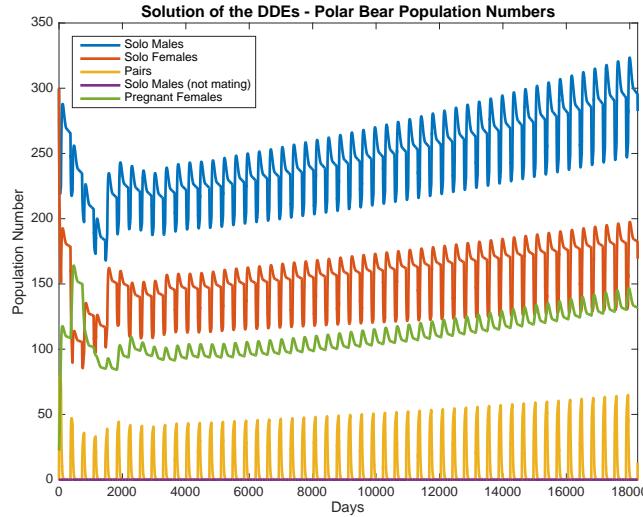


Figure 3.8: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 4.7 \times 10^{-5}$.

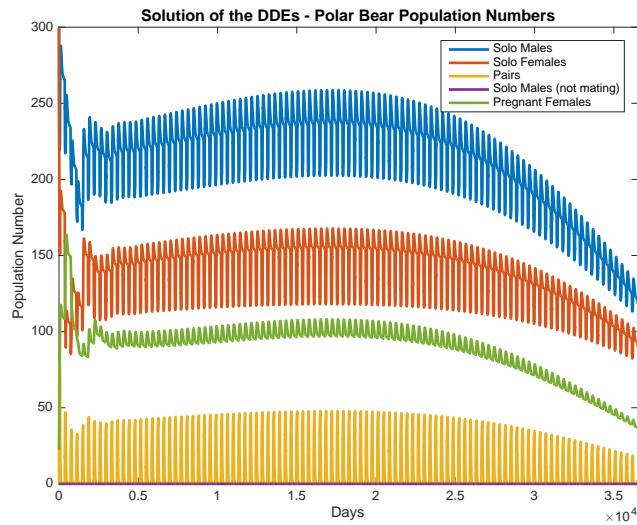


Figure 3.9: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 4.8 \times 10^{-5}$.

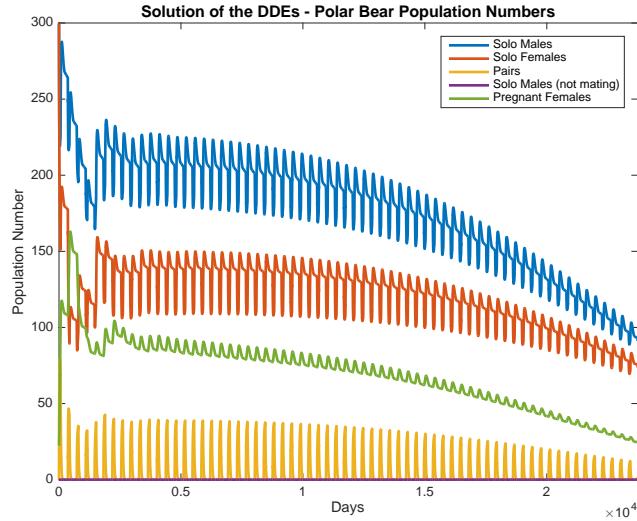


Figure 3.10: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 5 \times 10^{-5}$.

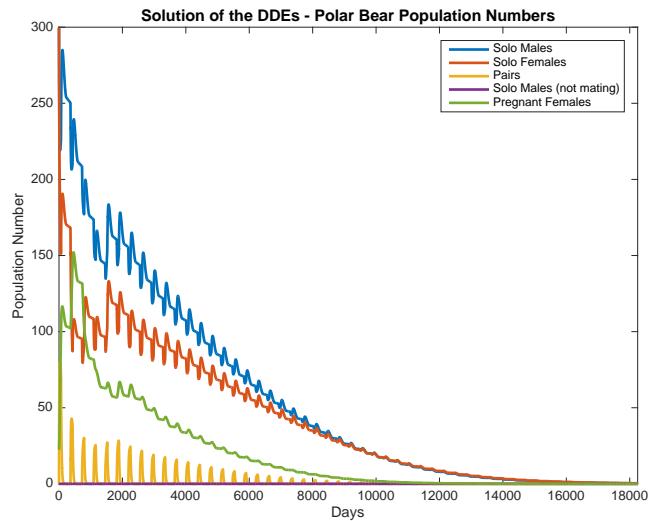


Figure 3.11: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 8 \times 10^{-5}$.

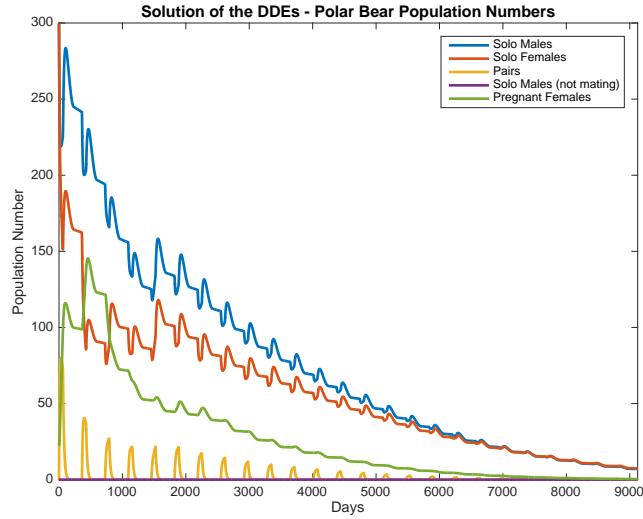


Figure 3.12: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 1 \times 10^{-4}$.

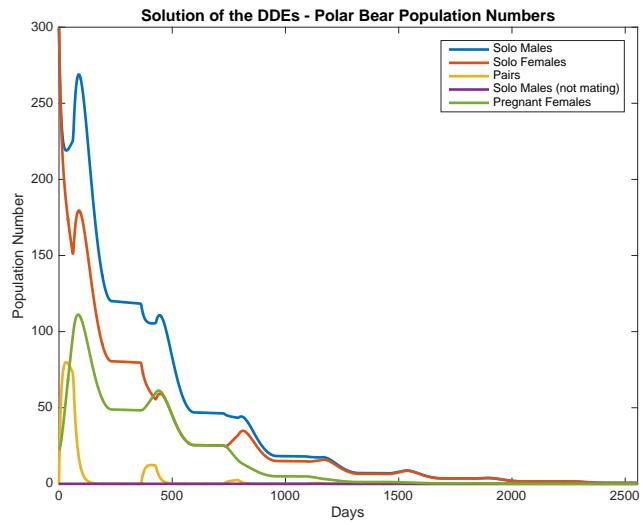


Figure 3.13: The solution to the system of DDEs (3.1) when the impact of temperature is $k = 5 \times 10^{-4}$.

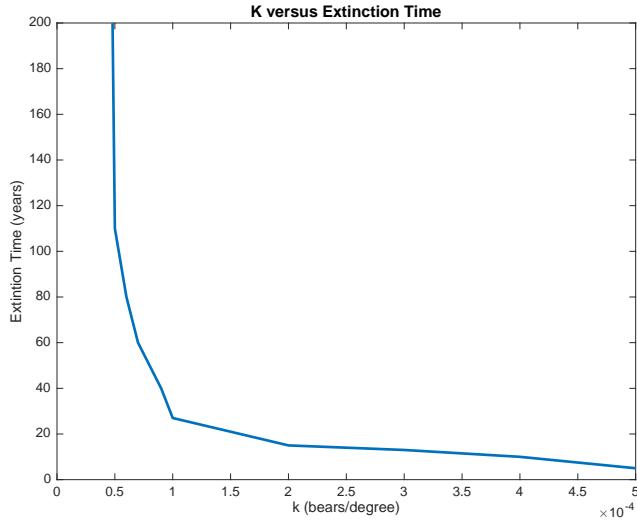


Figure 3.14: A plot showing k versus extinction time. All values less than 4.7×10^{-5} do not have extinction times as population growth is exponential.

Figure 3.14 displays a plot of the parameter k versus extinction time in years. This figure demonstrates the how all k values past the threshold impact the number of years to extinction. All values of k less than 4.7×10^{-5} do not have extinction times as population growth for these values is exponential.

3.5 Discussion

The warming climate in WH has been a cause for concern due to the decline in polar bear population numbers and their stability. The system of DDEs was able to represent the population density of bears in this region and predict how the increasing temperatures will effect the population growth. When temperature is not included in the system of DDEs it is clear that the population is increasing. Looking at only 1 year, the mating system of polar bears shows the population of solo males and females decreases as the paired and pregnant female population increases. There is a peak in the mating season that occurs around 30-40 days, which would represent the beginning to mid of April. Molnár et al. also observed a peak in mating during

mid-April thus confirming the consistency of the mating system used in our model [13]. Once the mating season ends the number of pairs returns to zero and the number of solo males, solo females and pregnant females remains relatively constant. The small increases occurring at the end of the year are a result of the residual mating time (i.e mating season can start 5 days prior to March 1st and end 5 days past the 60 day mating season). The number of solo males that do not continue mating during the mating season remains zero for all time. This is a result of us assuming the male mating ability, $\alpha = 1$, which implies all solo males will continue mate searching.

Once the increasing temperature was incorporated into the model, there are cases when the population growth was limited and population numbers reached extinction levels. The impact of k is clearly shown when observing Figure 3.14. The extinction times can be estimated for various levels of k . Increasing the number of bears per degree that are being lost has a decreasing effect on the extinction time. The curve demonstrates negative exponential behaviours. The impact of temperature on the death rates and survival rates of bears was varied to see how much of an impact the polar bear population could overcome. When the temperature increases are impacting the death rates at a very small proportion, $k = 1 \times 10^{-8}$, the population growth is identical to the case where temperature is not included in the model. Accordingly, the population number of solo males nearly doubles after 10 years, solo female numbers remain relatively constant and pregnant females numbers are almost 10 times the initial size. Thus, implying that if the impact of temperature remains at this level the population will remain stable. When the proportion is increased to $k = 1 \times 10^{-5}$ the population still increases. The rate of increase is slower which can clearly be seen. The number of solo males does not double, the solo female number is smaller than their initial number. However, pregnant females still grow to almost 10 times their initial size. This indicates that the polar bear population is still growing. However, the rate at which the population is growing has been decreased as a result of increasing temperatures.

When the effect of temperature is increased more the impact on the death rates and survival rates becomes too much and the population declines. It appears the threshold value of $k = 4.7 \times 10^{-5}$ is the last proportion that allows population growth. The population declines for the first few years, but is able to increase for the rest of time. The population numbers return to their initial values after the decrease and continue to increase at a rather slow rate. This could be explained by the death of solo males and females as result of climate change. Since the pregnant females are increasing during this time period the successful cubs are able to replace the males and females lost. Allowing the proportion to increase past this threshold to $k = 4.8 \times 10^{-5}$ the population is not able to withstand the impact of temperature. The simulations show the population numbers are approaching zero after 150+ years. The decline in population numbers occurs the fastest during the first few years and slows down as time goes on. The decrease in polar bear numbers is following a negative quadratic decrease. This indicates the population is not stable under this level of impact. When k was increased again to $k = 5 \times 10^{-5}$, the population declined rapidly for the first few years then slows down as time goes on. The decrease is still following a negative quadratic pattern and after 100+ years reaches extinction which is faster than the previous case.

Furthering the impact to $k = 8 \times 10^{-5}$ results in decreasing behaviour as above however the decreasing pattern is consistent for all time. The population numbers reach extinction level around 50 years. The population numbers are following an exponential decreasing pattern in the case. Similarly, when the proportion is given by $k = 1 \times 10^{-4}$ the population declines in an exponential pattern. The time to extinction in this case is approximately 25 years. Lastly, if the death and survival rates are impacted by temperature with proportion $k = 5 \times 10^{-4}$ the population does not survive past 5 years. The first year results in a rapid decline in population numbers. The number of both solo males and females decreases to less than half of their initial values. The pregnant females increase slightly but not enough to counteract the sudden loss of

males and females of reproduction age. Thus, it leads to the rapid extinction of polar bears.

3.6 Conclusion

The warming climate in the region of western Hudson Bay (WH) has been a concern due to the impacts it is shown to have on polar bear survival rates. By creating a continuous time model we were able to construct a system of delay differential equations that can be used to represent the population densities of polar bears. Incorporating the warming climate as a function that proportionally increases death rates and decreases survival rate, we were able to predict the future polar bear numbers under various impact levels. The advantages of using a continuous time model allows us to see the impact of mating directly and gives a clear picture of the seasonality of polar bear behaviours.

We were able to successfully model the mating system of polar bears throughout the years such that it followed the same patterns as the mating model used by Molnár et al. [13]. Without the impact of temperature, death rates and survival rates were constant and our model demonstrated that the polar bear populations would grow. The growth rate followed an exponential pattern. If a density-dependent death rate was used, we would expect the growth to be logistic. However, because the aim of this work is to identify how temperature increases will affect population numbers density-dependence was not needed.

When incorporating the impact of warming air temperatures to the death and survival rates we discovered a threshold value where if past this value population levels would decline. If the proportion of temperature impact remains below $k = 4.7 \times 10^{-5}$ the polar bears will be able to overcome the climate warming. The overall population numbers will be smaller than those without climate change however they will still be stable. If the proportion of temperature impact exceeds $k = 4.7 \times 10^{-5}$ then polar bears will not survive the climate change. If the

impact of climate change on both the death and survival rates is found to have this proportion of impact then population numbers will decrease. The decreases will continue until the polar bears are eventually extinct. The smallest proportion predicts polar bears could be extinct in approximately 150+ years and the largest predicts extinction after 5 years. With more data and information the exact proportion of impact could be determined and the model can be used to predict results more accurately.

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Chapter 4

Conclusions and Future Work

In this thesis, we studied the impact of climate change on polar bear population numbers. The increases in temperature in Western Hudson Bay (WH) have been linked to declines in bear survival. The use of time-dependent breeding and survival rates allowed for the investigation into how temperature could change these rates over a period of time. In Chapter 1, we reviewed the life cycle of polar bears to better understand the underlying population dynamics. We addressed the evidence of climate change and how it impacts polar bear life. We provided reviews of mathematical models that have already been done on this topic and state the objective of the thesis.

In Chapter 2, we created a matrix population model with time-dependent parameters. The use of discrete time allowed us to model the yearly population dynamics ignoring short term behaviours such as mating. The goal was to determine the long-term behaviour of the polar bear population. Numerical analysis of the model determined there are several simulations that resulted in polar bear extinction. In all scenarios that resulted in extinction the polar bear populations are unable to overcome the impacts of temperature increases. When the temperature increase followed concave down behaviour, the population was able to continue growing for several years before they succumbed to the temperature increases and declined toward extinc-

tion. When temperature exhibited concave up behaviours, the population was unable to grow and the population levels declined to extinction for all impact levels. For the polar bear population, this indicates that if temperature increases are to follow concave down behaviours the polar bears will be able to survive the impacts of climate change for several years. This could allow time for conservationists to determine appropriate strategies for saving the polar bears. Unfortunately, if the temperature follows the concave up behaviours the population will not survive.

When temperature increases impacted sub-adult polar bear survival more than prime-adult survival as suggested, the population extinction times were longer than if the survival rates were impacted equally. This suggests that prime-adults are able to survive long enough to have successfully weaned cubs. When the prime adults have enough cubs each year the population grows for sometime, but eventually the temperature impact will be too much and weaned cubs will not survive the sub-adult stage. The rate at which temperature increases and how it impacts the survival and breeding probabilities determines how long before population numbers reach zero. The best scenarios predict the population can overcome the temperature increases, while others predict extinction in 300 years or as early as 7 years. Under the current temperature trends, the model suggests we could see WH polar bear free in 50-80 years.

In Chapter 3, we created a system of delay differential equations (DDEs) in continuous time while ensuring the positivity of solutions. The model allowed us to model the short-term dynamics of polar bears, such as mating, to better understand the mechanisms underlying population growth. By using a continuous model, it allowed for the mating mechanism to be clearly seen throughout the years. The model allows for further studies that can incorporate Allee effects using density-dependence on mating and other parameters. One of the many advantages of a continuous time model is being able to see the population levels throughout the year and when they would be most sensitive to changes. Our model just looked at time-dependent death

and survival rates that were functions of temperature. The model created a framework that can be used to successfully capture the behaviours of polar bears throughout season. Numerical analysis determined that in the presence of climate change, polar bears are not able to survive once the level of impact surpasses a certain threshold value.

The polar bear population demonstrated population growth for the impact values under 4.7×10^{-5} bears per degree of increase. This indicates that polar bear populations are not in danger of extinction if the impact on their survival and death rates is within this range. When the impact value of bears per degree increased beyond 4.7×10^{-5} the polar bear population in WH is unable to survive the climate warming. The overall population numbers of polar bears will decrease until they reach extinction. The smallest proportion of impact suggests polar bears will reach extinction in 150+ years. This situation is a best case scenario since it gives us time to intervene and find a solution to the problem. The biggest impact showed the WH population would be extinct in 5 years. For polar bears, this means they are unable to survive with climate change. If the value of bears per degree can be estimated, we can have a better understanding about the future of polar bears in WH. The good news is if the value is currently below the threshold polar bears will be able survive the changes.

We were able to address certain aspects of the underlying problems facing the polar bears in WH region such as declines in survival. As further studies and future directions, one may include the other factors that are impacted by climate change. Some additional aspects include looking at habitat fragmentation and how it changes the male mating ability, pair formation and separation rates. For both Chapter 2 and 3, the use of density dependent parameters could be of interest to demonstrate Allee effects. Future directions could also include finding more extensive amounts of data that will fit the model accordingly. With more information on exactly how temperature impacts polar bears survival rates, the exact levels of impact can be determined and used for future projections of polar bear populations in other regions as well.

Curriculum Vitae

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