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Modeling the Effects of Harvesting on Virginia's Black Bear Population

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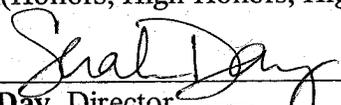
Modeling the effects of harvesting on Virginia's Black Bear population

A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelors of Arts / Science in **Mathematics** from
The College of William and Mary

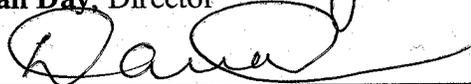
by

David William Gould

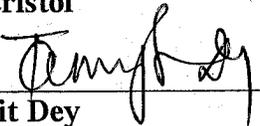
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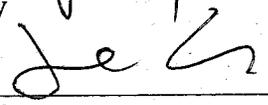
Sarah Day, Director



Dan Cristol



Tanujit Dey



Junping Shi

Williamsburg, VA
March 27, 2009

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Acknowledgments

This project was funded by the National Science Foundation under the following grants:

College of William and Mary, “UBM: Undergraduate Research in Metapopulation Ecology” (NSF #436318, PI: Cristol, Daniel)

College of William and Mary, “CSUMS: Theory, techniques, and research in computational mathematics ” (NSF #0703532, PI: Li, Chi-Kwong)

Many thanks are in order for the support of the NSF.

There are a great number of people without whom this paper would never have gotten off of its feet. It is my honor to acknowledge their contributions here. Initial work was inspired by a project written by Tristan Tronic, advised by Professor Junping Shi, on the dynamics of the Black Bear population [8].

If I have forgotten your name in this list, I beg your pardon! The weeks of writing a thesis has left me extremely scatterbrained. Know that I couldn't have written this paper without you, and that I am extremely grateful for the influence you had in shaping it!

First and foremost I would like to acknowledge the incredible amount of time that my adviser, Professor Sarah Day, has sacrificed to help me work on this project. I realize that with a baby on the way and three other Honors students you must have wanted to tear your hair on more than one occasion. I cannot express the amount of gratitude I have for the many hours I spent in your office whether it be getting advice on modeling, getting a pep talk, or just visiting. Thank you for everything that you've done from talking to me about Black Bears, to writing multiple letters of recommendation, to the chocolate cake you baked us many months ago. Your Ordinary Differential Equations class got me interested in math again, and working with you has inspired me to continue my studies.

Thanks as well to Professor Meagan Herald (who will probably always remain Professor McNulty to me)! I greatly appreciate the many hours spent in your office during the Summer of 2009. You provided me with a resource and an outlet during my summer research that you didn't have to provide. Thank you for the many hours spent in your office talking about Black Bears, Matlab code, LaTeX, and the nature of modeling. Also, thank you for the constant supply of baked goods during the summer - I tried to train Professor Day but to no avail. Although, she did make us chocolate cake on one occasion... Most importantly, thank you for telling me to put the Matlab code away for the weekend and to enjoy myself! The Environmental Modeling class

that you co-taught with Professor Cristol gave me a focus to my studies for which I am eternally grateful. I suppose that I forgive you for moving away to VMI, but I am still disappointed you weren't around during my Senior year. I hope all is well!

To Professor Junping Shi - thank you for getting me started with the Black Bear population. The resources and ideas that you provided at the beginning of the summer helped to shape my research project.

Additionally, thank you to all of the CSUMS and UBM faculty and staff from the Summer of 2009 - the program that you run is a great experience for undergraduates, and was extremely helpful in learning how to do research without the added stress of classes. In particular, I would like to thank Barbara Boyer and Marianna Williamson who had a large hand in keeping things running smoothly during the CSUMS summer program, I'm sure.

As for Kassie Archer, Brian Paljug, and Niha Zubair - what can I say? I was extremely fortunate to be able to work in the same summer program with you. You offered a constant source of amusement - Lyapunov (do doo dodo do), a certain someone's tendency to stalk anything and everyone, Bozeman Montana and the eternal shame that followed, breaking the deck in Montana (I'll never live that down), goofy babies, telling a small child that Kassie didn't like Professor Day, hacking into facebook profiles and leaving pictures in someone's mailbox, and many more things that I can't remember at this time. Most importantly, you weren't completely embarrassed to be seen with me in a public setting. Though the Georgia O'Keefe paintings are most likely seared into our subconscious, it was a pleasant work environment because of you all. Kassie - you and I went through thesis week together. Let us never again speak of the events that occurred in the Jones computer lab.

Thanks to Rafael Frongillo for helpful code that prevented me from having to learn C! Your help with GAIO and CHoMP is greatly appreciated! Know that Professor Day's students still harass her as much as you did.

Last, but certainly not least, thank you to my parents for being a constant source of support and comfort.

`\end{sappiness}`

Abstract

In 1999 the Virginia Department of Game and Inland fisheries developed a long term plan to manage the black bear population in Virginia; in 2001, the VDGIF published a 10 year management plan. Though the plan contained many ideas to manage the bear population - including fertility control, kill permits, regulated hunting, etc., the management proposal lacks any concrete insight as to the ramifications of these options. The models included in this paper aim to analyze the population dynamics of the Black Bear population in Virginia by using a non-linear discrete model which separates bears not only by age, but also by gender. Analysis on the models provide a great deal of insight as to the dynamics of the Black Bears. Additionally, initial data and model simulations suggest that the preservation of the male population is an important factor in maintaining the Black Bear species due to their increased harvest rates, something which is not accounted for in most of the literature concerning the preservation of the Black Bears.

Chapter 1

Introduction

1.1 Background

In 1999 the Virginia Department of Game and Inland Fisheries developed a long term plan to manage the Black Bear population in Virginia. The plan arose from numerous concerns including property damage (from bears in suburban areas), a conflict of interest between hunting groups and animal activists, and insufficient knowledge of population dynamics to properly manage the harvest of Black Bears in Virginia [4]. In 2001, the VDGIF published a 10 year management plan. Included in the plan are 8 main points of interest: population viability or persistence, desired population levels, habitat conservation, hunting seasons, ethics, homeowner conflicts, and non-hunting recreation. The Bear Management Plan contained many ideas to manage the bear population - including fertility control, kill permits, and other methods to regulate hunting [4]. While the management proposal discusses the implications of many methods in managing the Black Bear population, the addition of mathematical analysis allows a more complete exploration of the consequences of managing the population through harvesting.

A secondary study, also published in 2002, offered a wealth of information concerning the Black Bear population in Virginia. The study, called the Cooperative Alleghany Bear Study lasted from 1994 until 2000. Much of the data was published as part of a doctoral thesis written by Sybille Klenzendorf, entitled *Population dynamics of Virginia's Black Bear population*. Included in the thesis were harvest rates, survival rates, birthrates, sex ratios, and other measurements of the Black Bear population dynamics. The Cooperative Alleghany Bear Study was conducted in Northwestern Virginia, along the Southern Appalachians; the Northern study area was centered in Augusta and Rockingham counties, in addition to portions of Highland, Bath, Allegheny and Rockridge counties. A Southern Study area was also situated around the Mountain Lake Wilderness Area in Giles county [2] (Fig. 1.1). As such,

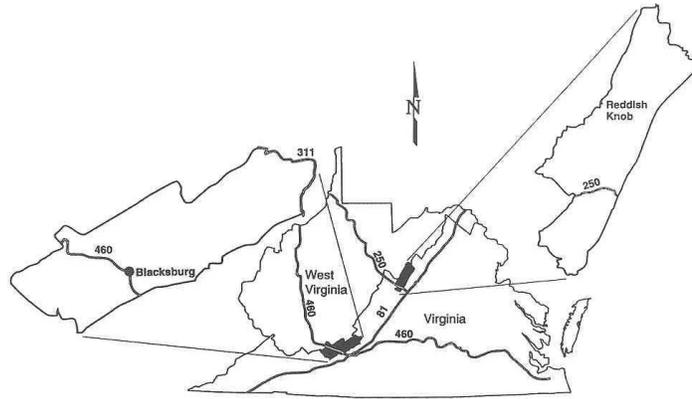


Figure 1.1: Northern and Southern Study Areas [2]

the parameters contained in the thesis are extremely useful for examining the Black Bear population along the Southern Appalachians.

Dr. Klenzendorf's thesis contains a mathematical model of the bear population. Using a Leslie Matrix Model with linear difference equations, the thesis tracks females through five age classes: Cub, First Years, Second Years, Third Years, and Adults [2]. Tracking only females in a population model is a fairly standard procedure; models yielded are lower in dimension than comparable models accounting for both males and females. Additionally, the insight can be just as useful. In this case, the elimination of males from the population does not provide a sufficiently accurate portrayal of the Black Bear population dynamics; the harvest rates provided in Dr. Klenzendorf's thesis demonstrate a marked difference between the harvest of male bears and female bears. For example, 45% of all two year old male bears were harvested, while only 22% of all two year old females were harvested in 2002. Additionally, three year old females have a harvest rate of 5%, while three year old males have a harvest rate of 30%. This, coupled with the projected 7.4% increase in total harvest per year [6] suggests that the size of the male Black Bear population may play a key role in determining the population's dynamics and the survival of the Black Bears.

The following models and the analysis thereof is geared specifically to analyze the effects of harvesting on the Black Bear population in Northern Virginia. Harvesting is here defined as the hunting of an organism for recreational purposes. More specifically, there is a particular interest in examining the relative importance of males and females within the breeding population. In general, females are seen as more important than males because one male can impregnate many females. Undoubtedly, females are needed in order to reproduce - the aim of this paper is not to dispute that. However, the higher harvest rates of males, as indicated by [2] suggest that, should no measures

be taken to preserve a reasonable breeding population of males, the population may decline.

There are three models examined in the paper. The first two are four dimensional systems of nonlinear difference equations - denoted as Basic Model Version 1 (Chapter 2, Section 2.3), and Basic Model Version 2 (Chapter 2, Section 2.4). The low dimensionality of the model comes from the compression of the standard age classes (Cubs, First Years, Second Years, Third Years, and bears older than three) into two categories - Subadults or Adults. The Basic Model Version 1 aims to analyze the Black Bear population under the effects of a harvest rate, given as a proportion of the population. While harvest rates become unrealistic with larger population sizes, they are more reasonable than constant harvest terms at smaller population sizes. Additionally, harvest rates allow for easier mathematical analysis in order to more fully understand the dynamics of the system. The second version of the Basic Model relaxes some assumptions made for the first version of the Basic Model by incorporating density dependence in survival, and utilizing a constant harvest instead of a harvest rate. A constant harvest is more accurate at higher population sizes - additionally, it allows for a better critique on using harvesting as a population management tool. We will also consider the incorporation of density dependent survival. Doing so restricts most of the mathematical analysis to numerical simulations which reveal intuition concerning the dynamics of the system. Finally, the last model is a 39 dimensional system of nonlinear difference equations which expands all of the standard age classes which were condensed in the Basic Models. The harvest constant is replaced with a weighted harvest rate, and the weighted survival rate is retained from the Basic Model. In addition, the Extended Model improves upon the Basic Models' birth term.

The following topics will be examined throughout the Chapters of this paper. In Chapter 2 the foundations of a Basic Model will be laid. Parameters, assumptions, and equations will all be explored. Chapter 3 establishes the Extended Model. Finally, in Chapter 4 the analysis gained from both the basic and the Extended Model will be used to look at the relative importance of bear gender/age categories with regard to the preservation of the population under the effects of harvest. Additionally, there will be an overall critique of the current management plan for the Black Bear population, with suggestions based on the results of model simulations.

1.2 Summary of Results

Basic Model Version 1

The first version of the Basic Model has up to two steady state solutions - for almost all biologically relevant parameter values there exists the zero solution, and a non zero steady state solution. There is a special case in which only the zero solution exists, but it remains mostly irrelevant to the analysis of the Black Bear population. When both equilibria exist, the zero solution is locally asymptotically stable (a sink), and the non zero solution is unstable for all biologically relevant parameter values. In particular, it is a saddle point with one or two unstable directions dependent upon initial parameters. The harvest rate (here a percentage of each age/gender category) was allowed to increase by 7.4% per year [6]. Simulations reveal that the amount of increase necessary to cause the population to decline towards extinction was dependent upon the initial condition – for an initial total population size of 9,500 bears, it took only 2 years of growth in harvest rate for the solutions to limit towards extinction. For higher initial population sizes, longer periods of growth in the harvest rate were required to cause the population to tend towards extinction. For some initial conditions no amount of growth in harvest rate caused the extinction of the population.

Basic Model Version 2

The second version of the Basic Model has the zero steady state solution, as well as an apparent periodic solution which does not appear sensitive to initial conditions. It may fulfill the necessary conditions to be globally stable for all initial conditions, and a broad range of harvest values. In the Basic Model Version 2 a constant harvest (units of bears) was used instead of a harvest rate (a percentage of the population). The code was designed in such a way that the harvest only began after 10 years, allowing the solutions to enter the periodic orbit before being subject to harvesting. For a constant harvest of 0 bears, the solution was unstable but, as the harvest constant increased, the periodic solution appeared to become stable. Two cases are examined - homogenized harvest across all gender/age classes (the same number is subtracted from each age/gender category), and a harvest constant which is a percentage of some fixed total harvest. The second case was used to make a more realistic distribution of harvest constants to mirror the differing harvest rates found by Klenzendorf [2]. For example, a total harvest might be 1,000 bears. Then, a percentage of 1,000 would be subtracted from one age/gender category, another percentage from a second

age/gender category, etcetera, such that all percentages summed to 1. If the system is allowed to reach its orbit before harvesting occurs, it took a total harvest pool of 870 bears divided amongst the Subadult and Adults to cause the population to tend towards extinction. For small initial conditions, it took longer for the solutions to enter its orbit, and the harvest began well before the solution entered its orbit. These cases may have given slightly less realistic results to be used to critique the management plan. However, this version of the model was designed to look at larger population sizes.

The Extended Model

Through initial numerical experiments, it appears that the Extended Model also has nonzero steady state solution which is locally asymptotically stable, if not globally stable, for all initial conditions - it appears to be a sink. The weakness in the Extended Model concerns the manner in which harvest is increased in the simulation. The harvest constant was replaced with weighted harvest, which is a function of a harvest rate and the total population. The increase in harvest is done through the harvest rate, which changes the behavior of the weighted harvest, sometimes creating unrealistically high harvest proportions. As this occurs, the what appears to be a nonzero steady state solution is driven closer to the zero equilibrium. Nevertheless, the density dependent effects add validity to the model. It takes 12 years of increase in the harvest rates in order to cause the Black Bear population to tend towards extinction for any initial condition. The most interesting aspect of this model is that it shows that the harvest of the Males in the population directly leads to the extinction of the population; if the harvest rate of males is allowed to remain constant (and hence X does not change for the male equations), then 12 years of growth in harvest rates is not enough to cause the population to go towards extinction.

Overall, all three models provide useful analysis which can be used to analyze the management plan for the Black Bear population set out by the Virginia Department of Game and Inland Fisheries - the most important of which is demonstrating that, while females are important for the preservation of the species, there needs to be some mechanism which allows the breeding male population to retain enough members to sustain the population through new births.

Chapter 2

The Basic Model

2.1 Population Dynamics

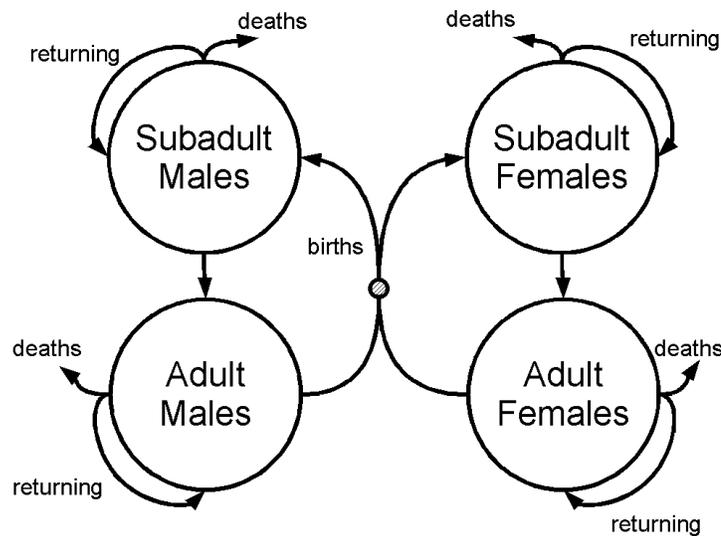


Figure 2.1: Dynamics of the Bear Population in the basic model

The Black Bear population is generally divided into five different categories, such as in [2]. These categories are Cubs, First Year bears, Second Year bears, Third Year bears, and Adult bears. These divisions are made due to differences in survivability, harvesting, and fecundity. The Basic Models (Version 1 and 2) aim to examine the Black Bear population using a system of nonlinear difference equations with a minimal number of dimensions. Towards this end, these different age categories are condensed into four age and gender classes as denoted in Figure 2.1.

The Subadults encompass bears from birth until the age of two at which point they mature into the Adult population. From this point forward, let First Year Bears be those bears which are one year old, Second Year Bears be those bears which are two years old, and Three Year Bears be those bears which are three years old. There is no specific name for the pool of bears which are older than three years old - they

are included in the Adult male and female category shown in the flow chart, along with the Third Years. Notice that there is an arrow feeding back into the SubAdult population - this is necessary to ensure that only a certain proportion of the bears (those that mature from Second Year bears into Third Year bears) mature into the Adult age category. Each of the categories depicted in Figure 2.1 are designed to have a certain proportion of of each age class within them. A certain proportion of the Subadult bears count as Cubs, another proportion as First Year males, and another proportion as Second Year males. Similarly, in the Adult male population, a certain proportion are Third Year males, and the rest are age four and over.

This could most easily be compared to a Lefkovich stage class matrix model - often associated with modeling sea turtles. This model type is often used for organisms which may take longer than one year to mature into a higher age category. In this case, Subadult bears do not remain as Subadults for varying amounts of time biologically. Rather, this is a mechanic introduced in order to reduce the dimension of the model while retaining as many dynamics of a full model as possible.

As mentioned in the Introduction, modeling both male and females separately is a necessary dynamic to fully understand the implications of harvesting the Black Bear population. This mainly has to do with the different harvest rates encountered between the male and female bears found by Dr. Klenzendorf [2]. Indeed, it is even mentioned that male bears might be more easily harvested due to their higher dispersal rate [2].

In general, the equations whose dynamics are shown in Figure 2.1 should be thought of as follows:

$$\text{Subadult females} = \text{females born} + \text{survival of female Cubs}$$

$$+ + \text{survival of First Year females}$$

$$\text{Subadult males} = \text{males born} + \text{survival of male Cubs}$$

$$+ \text{survival of First Year males}$$

$$\text{Adult females} = \text{Second Year females which mature} + \text{survival of Third}$$

$$\text{Year females} + \text{survival of older females}$$

$$\text{Adult males} = \text{Second Year males which mature} + \text{survival of Third}$$

$$\text{Year females} + \text{survival of older males}$$

The following sections will expand upon these equations and will note parameters

as necessary.

2.2 Overview of Parameters

The main parameters of interest in the Basic Model include the natural survival rates, the harvesting rates per year per age/gender class, and pertinent reproductive rates. An exhaustive list of parameters can be found in the Appendix A.5. A brief overview of the main parameters are included here, as well as their method of calculation. Most are derived from the information obtained in Dr. Klenzendorf's thesis [2].

Among the parameters listed in the Appendix A.5, the harvest rates are the most reliable. Harvest information for Cubs and one year old bears, however, were not discussed. The harvest data for Cubs is nonexistent because it is illegal to hunt female bears with Cubs [4]; an idealized harvest rate of 0% for Cubs is used in the model. The parameters used for the First Year bear harvest rates are rough estimates. Because bears stay with their mothers for around one and a half years after birth, and Cubs are usually born in early December [4], First Year bears would leave their mothers 6 months following their first birthday. The hunting periods occur between October and December; thus, First Year bears are not protected under Virginia legislature. On the other hand, the desirability of First Year bears (in terms of harvesting) is questionable due to their relatively small size. As such, a conservative harvest rate of 5% was chosen for the First Year bears.

The natural survival rates of Black Bears - excluding harvest, old age, and events such as vehicular accidents - were well documented for Cubs [5], and Second Years and up [2]. Dr. Klenzendorf projects non-hunting season survival rates as 0.998 for Second and Third Year females, 0.995 for females older than three, and 1.00 for all male bears in the Second Year and older. This agrees with the statement that survival rates for most of the older bears (of both genders) are very close to 100% [5]. Unfortunately, the relatively small sample population used in [2] limits the ability to generalize the survival rates the bears at the study cite are not at capacity and lack competition for resources and territory. The utilization of these survival rates for a model is not unreasonable if we assume the population simulated is under carrying capacity and we include some mechanism to eliminate bears from the population due to old age.

Two sub-age classes have escaped mention thus far. For Cubs, the VDGIF estimates a survivability of approximately 80% [5]. Unfortunately, very little data exists

on the survivability of First Year bears (both male and female). As such, they have been estimated at around 85% for both males and females. A better estimate for First Year bear survivability is needed to enhance the model's accuracy.

Harvest rates are used in two ways throughout this paper. The first version of the Basic Model as well as the Extended Model both consider harvest rates as a percentage of the population. Using a harvest rate (taking a fixed proportion of the population as harvested per year) allows the harvest to scale with population changes that may change the amount of effort expended by a hunter to harvest one bear. For relatively small population sizes a hunter would, perhaps, need to spend more time seeking a suitable bear for harvest than if the population was large. Thus, at smaller population sizes at least, a harvest rate serves as an adequate method to track the harvest of a population. Problems arise when the population grows extremely large - if there were 50,000 Second Year bears then it makes little sense to be able to harvest 45% of them in one year. The Basic Model Version 1 makes more valid predictions at smaller population sizes. The Basic Model Version 2 will consider harvest as a constant number of bears which are subtracted from each of the four age classes separately. This method allows for more analysis to be made which directly corresponds to a management plan. The only downfall of using a constant harvest has to do with the lack of information in the examined literature. There are estimates, per the VDGIF, of the exact number of bears harvested in a given year [6]. However, these estimates do not distinguish between age. Any resulting constant harvest would be an arbitrary estimate.

The final set of parameters which are fully dependent on experimental data are the birth terms. Normally Adult female and Third Year female bears reproduce every other year, as mentioned previously in this paper, and explained in more detail in [4]. The Management plan also mentions that females may reproduce in consecutive years, should the first litter be lost. This is a concept which Klenzendorf also examines through the course of her thesis. The data yielded from the study of female bears in the Northern and Southern study sites indicate that approximately 55% of female bears reproduce every year due to loss of litter, where ideally only 50% would reproduce each year [2]. This value is built in to the model as a parameter. Thus far all simulations use 55% as the parameter value, but altering how many females reproduce each year could have substantial consequences on the overall population model, and should be considered in future simulations. Adult female bears have an average litter size of 2.35 Cubs; Third Year female bears have a litter size of approximately 1.1 Cubs [2]. Female bears younger than three years of age may attempt to

breed but, according to the Black Bear Management Plan, none are known to have successfully raised litters of Cubs [4].

All parameters stated thus far have additional restrictions which limit their validity. First and foremost, the data expressed in Dr. Klenzendorf's thesis are only valid between the years 1994 and 2002 - the years when Cooperative Allegheny Bear Study was being conducted. Undoubtedly, environmental factors play a huge part in the values given to the parameters; currently there are no parameters which take this into account. It should be noted, however, that for many of the values obtained from Dr. Klenzendorf's thesis, there was no correlation between survival/birthrates and soft mast production (fruits and nuts) [2]. However, because the population was assumed to be under carrying capacity, the Black Bears in the area may not have needed to compete for resources even taking into account low soft-mast production. Even so, the lack of correlation between survival/birthrates and soft mast production lessons the weakness that omitting environmental changes entails.

2.2.1 Proportions within the age/gender classes

One other set of parameters warrants mention in this section. In Section 2.1 it was mentioned that the Subadults contained a certain proportion of Cubs, First Years, and Second Years and that Adults contained a certain proportion of Third Year bears and bears older than three. For example, it could be assumed that the Subadult male population is $\frac{1}{3}$ Cubs, $\frac{1}{3}$ First Year males, and $\frac{1}{3}$ Second Year males. The Adult male population might be $\frac{1}{2}$ Third Year males and $\frac{1}{2}$ males older than three. Any division of the bears into these sub-age classes would be purely arbitrary as no exact proportions have been encountered in the literature thus far. Let us assume that we have information on a steady state distribution of Cubs, First Year bears, Second Year bears, Third Year bears, and Adults for both male and female bears without the effects of harvesting. One would be able to find the proportion of Cubs relative to those age categories which are included in the Subadult class. In other words:

$$\text{Proportion of Cubs in Subadult} = \frac{\text{Number of Cubs}}{\text{Number of Cubs} + \text{Number of First Years} + \text{Number of Second Years}}$$

This procedure would then be repeated for each age and gender category in the Subadults (Cubs, First Years, and Second Years) as well as each category in the

Adults (Third Years, Adults). The Adults, as a reminder, include both Third Year bears and Adult bears.

In this case, the apparent stable age distribution is found from a numerical simulation of the Extended Model (Chapter 3). The results of the simulation can be seen in Figure 3.7. The proportions will be dealt with more explicitly in Section 2.3.2, and can be found in Appendix A.5.

2.3 Basic Model Version 1

2.3.1 Assumptions

In addition to the matters examined in Section 2.2, there are other assumptions which warrant further exploration.

The largest assumption of the Basic Model Version 1 has to do with the lack of density dependent effects. If we assume that the Black Bears being examined by the following model have a total population size of less than 75% of some carrying capacity, K , then we can assume that density dependence does not affect the population. This is based on [7] referenced in [2] and was used to justify the lack of density dependent effects in the modeling encountered in [2]. It should be noted that [7] examines a polar bear population when it uses this argument. However, they cite two arguments which argue that “the effect of increased number is minimal at low and intermediate densities for long-lived animals with delayed reproduction”. This argument would extend to the Black Bear population.

The method in which the Subadults and Adults are subdivided into Cubs, First Year Bears, Second Year Bears, Third Year Bears, and bears four years of age and older also puts some limitations on the validity of the results of the Basic Model. As will be seen in the equations, the parameters used to divide the Subadults into Cubs, First Years, and Second Years are constants. These proportions force the Subadult and Adult populations to contain a certain percentage of each of these sub age categories at all population sizes. Then, at any given iteration of the simulation, there may be more bears which are subject to the First Year male harvest rate than there would actually be in the population. Alternatively, there may be less bears subject to the First Year male harvest rate than there would actually be. One would expect that, if each of these sub-age classes were independent of the other sub-age classes - that is, if each sub-age class had its own equation, that a high harvest rate for First Year males would cause the First Year male population to be lowered. The low number of First Year males that survive would then yield a low Second Year male

population, and so on. For example, let us say that there are 99 Subadult males, and that they are divided equally into Cubs, First Years, and Second Years. So, there are 33 of each sub-age class; additionally, there are 55 births each year. Say that Cubs are not harvested, First Years have a harvest rate of $\frac{1}{3}$, and Second Years have a harvest rate of $\frac{2}{3}$. The surviving Second Year Bears mature into the Adult Population and are no longer counted as Subadults. Finally, assume there is a 100% survival rate for all sub-age classes. Recall the basic dynamics of the system should reflect the following:

$$\begin{aligned} \text{Subadult females} &= \text{females born} + \text{survival of female Cubs} \\ &\quad + \text{survival of First Year females} \end{aligned}$$

$$\begin{aligned} \text{Subadult males} &= \text{males born} + \text{survival of male Cubs} \\ &\quad + \text{survival of First Year males} \end{aligned}$$

$$\begin{aligned} \text{Adult females} &= \text{Second Year females which mature} + \text{survival of Third} \\ &\quad \text{Year females} + \text{survival of older females} \end{aligned}$$

$$\begin{aligned} \text{Adult males} &= \text{Second Year males which mature} + \text{survival of Third} \\ &\quad \text{Year females} + \text{survival of older males} \end{aligned}$$

Iterations of the code as used in the Basic Model Version 1 would be the following:

Iteration 0:

$$\text{Total Subadult males} = 99$$

$$\text{Cubs} = \frac{1}{3} * 99$$

$$\text{First Years} = \frac{1}{3} * 99$$

$$\text{Second Years} = \frac{1}{3} * 99$$

Iteration 1:

$$\text{Total Subadult males} = \text{New Births} + \text{All Cubs} + (1 - \frac{2}{3}) * 33$$

$$\text{Total Subadult males} = 55 + 33 + 11 = 99$$

Iteration 2:

Based on this, the division in this iteration would be

$$\text{Cubs} = \frac{1}{3} * 99$$

$$\text{First Years} = \frac{1}{3} * 99$$

$$\text{Second Years} = \frac{1}{3} * 99$$

$$\text{Total Subadult males} = \text{New Births} + \text{All Cubs} + (1 - \frac{2}{3}) * 33 + (1 - \frac{1}{3}) * 33$$

$$\text{Total Subadult males} = 55 + 33 + 11 = 99$$

And so on.

Note that at each iteration the number of male Cubs, First Year males, and Second Year males remains the same. Were we to use a scheme which expands each sub-age class into its own equation (with a more traditional Leslie Matrix model), then we would see something similar to the following:

Iteration 0:

$$Cubs(0) = 33$$

$$First\ Years(0) = 33$$

$$Second\ Years(0) = 33$$

$$Third\ Years(0) = 0$$

$$Total\ Subadult\ males(0) = 99$$

Iteration 1:

$$Cubs(1) = New\ Births(1) = 77$$

$$First\ Years(1) = (1 - 0)*Cubs(0) = 33$$

$$Second\ Years(1) = (1 - \frac{2}{3})*First\ Years(0) = 11$$

$$Third\ Years(1) = (1 - \frac{1}{3})*Second\ Years(0) = 22$$

$$Total\ Subadults\ males(1) = Cubs(1) + First\ Years(1) + Second\ Years(1) = 121$$

Iteration 2:

$$Cubs(2) = New\ Births(2) = 77$$

$$First\ Years(2) = (1 - 0)*Cubs(1) = 77$$

$$Second\ Years(2) = (1 - \frac{2}{3})*First\ Years(1) = 11$$

$$Third\ Years(2) = (1 - \frac{1}{3})*Second\ Years(1) \approx 14$$

$$Total\ Subadults\ males(2) = Cubs(2) + First\ Years(2) + Second\ Years(2) = 165$$

And so on.

The differences between the two methods are apparent - the former retains the same population size each iteration, while the more traditional Leslie Matrix scheme more accurately keeps track of the trickle-down effect of individual age class harvest rates. The former is chosen for the low dimensional model yielded. Because the goal is to capture the dynamics of the expanded Leslie Matrix model, the proportions of Cubs, First Year bears, and Second Year bears were based on an apparent steady state solution of the Extended Model mentioned in Chapter 3, Figure 3.7. The assumption is that, by using information from a known steady state solution, the Basic Model best reflects the dynamics of the Extended Model - a full Leslie Matrix Model.

In particular, consider that the Second Year males have the highest harvest rate per the literature [2]. Given the nature of the Basic Model Version 1, it does not make sense for an equal $\frac{1}{3}$ division of the Subadult males into the Cubs/First Years/Second

Years. More bears in the Basic Model Version 1 are subject to the higher Second Year harvest rate than would be in a model which accounts for all age classes individually. It was previously mentioned that the proportions used to determine the number of Cubs in the Subadults was based off an apparent steady steady solution from the Extended Model. In the Basic Model Version 1, the proportion of Second Year males within the Subadult male population is relatively low compared to the male Cubs and the First Year males. In turn, this only subjects a low proportion of Subadult males to the higher Second Year male harvest and more accurately reflects the behavior of the Leslie Matrix model described above.

2.3.2 Equations

With the current information we can formulate a low dimensional model which may give insight to the dynamics of the bear population. Recall the basic

Let us first examine the Subadult females.

$$S_{f,t+1} = \underbrace{0.5 * p_f * b_t * \beta_1 * v_{tf} * A_{f,t} * A_{m,t} + 0.5 * p_f * b_a * \beta_2 * v_{af} * A_{f,t} * A_{m,t}}_{\text{number of Cubs from Third Year females + number of Cubs from Adult females}} + \underbrace{(s_{cf} - h_{cf}) * v_{cf} * S_{f,t}}_{\text{number of surviving Cubs}} + \underbrace{(s_{ff} - h_{ff}) * v_{ff} * S_{f,t}}_{\text{number of surviving First Year females}}$$

The terms, in the order in which they appear, are:

$S_{f,t}$ – Subadult female Bears at time t.

p_f – The proportion of females that breed in any given year.

b_t – The birthrate of Third Year females.

β_1 – A term which weights the number of Cubs for Third Year females.

β_2 – A term which weights the number of Cubs for Adult females.

$A_{m,t}$ – Adult male Bears at time t . This category includes any male bear which is three years of age, or older.

$A_{f,t}$ – Adult female Bears at time t . This category includes any female bear which is three years of age, or older.

v_{xy} – The proportion of age class x , and gender y . Recall that Cubs, First Year Bears, and Second Year Bears are considered Subadults.

$x \in \{\text{Cubs } (c), \text{First Year Bears } (f), \text{Second Year Bears } (s),$

Third Year Bears $(t), \text{Adults } (a)\}$,

$y \in \{\text{males } (m), \text{females } (f)\}$.

b_a – The birthrate of female bears above the age of three.

s_{xy} – The survival rate of age class x and gender y , where x and y are defined as above.

h_{xy} – The harvest rate of age class x and gender y , where x and y are defined as above.

All of the parameter values can be found in Appendix A.5.

The terms $- 0.5 * p_f * b_t$ and $0.5 * p_f * b_a$ both give the number of bears which are born in a given year. Based on the literature we can say that there is a 1:1 Male:Female split in the Cubs born in a given year - this is why each of the birth terms are multiplied by 0.5 in the beginning. Recall also that only 55% of the female bears breed in any given year - this is in the term p_f . These terms then multiply $\beta_1 * v_{tf} * A_{f,t} * A_{m,t}$ and $\beta_2 * v_{af} * A_{f,t} * A_{m,t}$.

$v_{tf} * A_{f,t}$ yields the number of Adult females which are considered Third Year females. Similarly, $v_{af} * A_{f,t}$ yields the number of Adult females which are older than three. β_1 and β_2 both scale the birthrates so that an explosion of Cubs based on the nonlinear term $A_{f,t} * A_{m,t}$ does not occur for low and moderate population sizes. Though using a basic quadratic birth term does not provide the best solution, it adequately ensures that there cannot exist Cubs without both males and females. The β_1 and β_2 terms are derived as follows:

Assume X is the number of Adult females which are considered Third Year females, Y are the number of Adult females older than three, and Z is the number of

males. At these population values, assume that the following is true:

$$b_t * \beta_1 * X * Z = b_t * X$$

and

$$b_a * \beta_2 * Y * Z = b_a * Y.$$

That is to say, at X , Y , and Z we are assuming that there are exactly $b_t * X$ and $b_a * Y$ Cubs being born to Third Year females and females older than three, respectively. For the model, it is assumed that $X = Y = Z = 1,000$. Thus, $\beta_1 = \beta_2 = \frac{1}{1,000}$.

The rest of the terms are, for the most part, self explanatory - terms such as $s_{xy} - h_{xy}$ give the survivability of age class x and gender class y after harvesting is taken into account. Note that the equation for Subadult males ($S_{m,t}$) is identical to the Subadult females, with different parameter values.

Now, examine the equation for Adult females.

$$A_{f,t+1} = \underbrace{(s_{sf} - h_{sf}) * v_{sf} * S_{f,t}}_{\text{number of matured Second Year females}} + \underbrace{(s_{tf} - h_{tf}) * v_{tf} * A_{f,t}}_{\text{number of surviving Second Year females}} + \underbrace{(s_{af} - h_{af}) * v_{af} * A_{f,t}}_{\text{number of surviving bears above age three}} .$$

The terms are all defined as above. The equation for the Adult males mirrors the equation for the Adult females - note they are both linear.

2.3.3 Analysis

For all intents and purposes, the parameters encountered in the aforementioned equations for Subadults and Adults can be condensed into single terms.

$$S_{f,t+1} = b * A_{f,t} * A_{m,t} + c * S_{f,t}$$

$$S_{m,t+1} = b * A_{f,t} * A_{m,t} + d * S_{m,t}$$

$$A_{f,t+1} = e * S_{f,t} + f * A_{f,t}$$

$$A_{m,t+1} = g * S_{m,t} + h * A_{m,t}.$$

Where

$$\begin{aligned}
b &= 0.5 * p_f * b_t * \beta_1 * v_{tf} + 0.5 * p_f * b_a * \beta_2 * v_{af} \\
c &= v_{cf} * (s_{cf} - h_{cf}) + v_{ff} * (s_{ff} - h_{ff}) \\
d &= v_{cm} * (s_{cm} - h_{cm}) + v_{fm} * (s_{fm} - h_{fm}) \\
e &= v_{sf} * (s_{sf} - h_{sf}) \\
f &= v_{tf} * (s_{tf} - h_{tf}) + v_{af} * (s_{af} - h_{af}) \\
g &= v_{sm} * (s_{sm} - h_{sm}) \\
h &= v_{tm} * (s_{tm} - h_{tm}) + v_{am} * (s_{am} - h_{am}).
\end{aligned}$$

These equations describe a map,

$$F : \mathbb{R}^4 \rightarrow \mathbb{R}^4$$

Consider

$$\Omega = \{(S_m, S_f, A_m, A_f) \mid S_m, S_f, A_m, A_f \geq 0\}.$$

We aim to show that $F : \Omega \rightarrow \Omega$ if b, c, d, f, g, h are positive. Based on the parameter values (Appendix A.5):

$$\begin{aligned}
b &\approx 6.15 * 10^{-4} & c &\approx 0.7425 \\
d &\approx 0.7425 & e &\approx 0.0557 \\
f &\approx 0.8750 & g &\approx 0.0395 \\
h &\approx 0.7999
\end{aligned}$$

At the very least, for parameters found in the literature we can say $F : \Omega \rightarrow \Omega$.

In general, $0 \leq s_{xy} \leq 1$ and $0 \leq h_{xy} \leq 1$ because they are both proportions of the Black Bear population. Biologically, it only makes sense to also have $0 \leq s_{xy} - h_{xy} \leq 1$ because one can never harvest a higher proportion of bears than the proportion that survive in any given year. Any values for the survival and harvest rates would have no biological relevance, and are safeguarded against in the Matlab code. As such, for all parameters to be used in the system, $b, c, d, f, g, h, j \geq 0$ which allows the statement that

$$F : \Omega \rightarrow \Omega$$

for all relevant parameter values.

We can solve for S_m, S_f, A_m, A_f to be the following, based on the previously mentioned system of equations.

$$S_m = \frac{b * A_f * A_m}{1 - c} \qquad S_f = \frac{b * A_f * A_m}{1 - d}$$

$$A_m = \frac{g * S_m}{1 - h} \qquad A_f = \frac{e * S_f}{1 - f}.$$

Given $c, d, f, h \neq 1$.

It is never the case that $c, d, h, f = 1$ for the set of parameters relevant for this model. Examine,

$$c = v_{cf} * (s_{cf} - h_{cf}) + v_{ff} * (s_{ff} - h_{ff})$$

Recall that $1 \leq s_{xy} - h_{xy} \leq 1$, thus the maximum value of c is $v_{cf} + v_{ff}$. Recall that both the Cubs and the First Year bears are considered part of the Subadult population in addition to the Second Year bears. Thus, it must be true that $v_{cf} + v_{ff} + v_{sf} = 1$ where v_{cf} is the proportion of female Cubs in the Subadult female population, v_{ff} is the proportion of First Year females in the Subadult female population, and v_{sf} is the proportion of Second Year females in the Subadult female population. In c above, only the term for female Cubs and female First Years are included. Again, there is no biological relevance for setting $v_{sf} = 0$ because, if this were true, then none of the Subadult females would transition into the Adult female population. Thus, $v_{cf} + v_{ff} < 1$. Thus it is ensured that the aforementioned parameters are not equal to 1 for all possible parameter values to be used in this system.

It can be shown that, given $S_{m,t}, S_{f,t}, A_{m,t}, A_{f,t} \neq 0$:

$$S_m = \frac{(1-f) * (1-d) * (1-h)}{b * e * g}$$

$$S_f = \frac{(1-f) * (1-c) * (1-h)}{b * e * g}$$

$$A_m = \frac{(1-f) * (1-d)}{b * e}$$

$$A_f = \frac{(1-c) * (1-h)}{b * g}.$$

Special cases occur when $b, e, g = 0$.

If $b = 0$ the only steady state solution is the zero solution. We can see that $b = 0.5 * p_f * b_t * \beta_1 * v_{tf} + 0.5 * p_f * b_a * \beta_2 * v_{af}$ would be driven to zero only if the percentage of females which breed in a given year, p_f , or the birthrates of Third Year females and females older than three, b_t and b_a respectively, are driven to zero. While this could occur, it is unlikely given the data from the current literature.

There exists a bifurcation in the number of steady state solutions when $b = 0$. At $b = 0$ the only steady state solution that exists is \bar{X}_0 . When $b > 0$, some $\bar{X}_1 \neq \bar{0}$ also exists.

It might be the case that e or g equal 0 based on parameter choices - $s_{xy} - h_{xy} = 0$ indicates a harvest of the entire sub-age class. While unlikely, it is not an improbable situation. Consider the survival and harvest of Second Year males and females: if either $s_{sy} - h_{sy} = 0$ (where $y \in \{\text{males (m)}, \text{females (m)}\}$), then there is no transfer of the Subadult males and/or females into the Adult male or female population respectively. Bifurcations in the number of steady state solutions also exist for the case when $e, g = 0$; if $e, g = 0$ then $\bar{X}_0 = \bar{0}$ is the only steady state solution. The code does not guard against this occurrence.

The parameter values from the literature, found in the Appendix A.5, yield values for b, c, d, e, f, g, h which are both nonzero and less than one which ensure that there are two distinct steady state solutions - the zero solution, and a nonzero solution shown below.

$$S_m \approx 4,762.4$$

$$S_f \approx 4,762.4$$

$$A_m \approx 939.324$$

$$A_f \approx 2,123.$$

Let $\bar{X}_1 = (4762.4, 4762.4, 939.324, 2123)$, the nonzero steady state solution. The Jacobian of the system is as follows:

$$J = \begin{pmatrix} c & 0 & b * A_f & b * A_m \\ 0 & d & b * A_f & b * A_m \\ g & 0 & h & 0 \\ 0 & e & 0 & f \end{pmatrix}$$

Once evaluated in Matlab, the eigenvalues of the Jacobian evaluated at \bar{X}_1 are:

$$\text{Eigenvalues} = \begin{pmatrix} 1.0810 \\ 0.8445 \\ 0.7425 \\ 0.4915 \end{pmatrix}$$

Because the maximal eigenvalue, $\|\lambda\| = 1.0810$ is greater than one, the steady state solution is unstable and sensitive to initial conditions. Because the other eigenvalues are all less than one in magnitude, the behavior of solutions around \bar{X}_1 should be that of a saddle with three contracting directions and one expanding. There is expansion in the S_m direction, and contraction in the S_f, A_m, A_f directions.

The eigenvalues evaluated at \bar{X}_0 are

$$\text{Eigenvalues} = \begin{pmatrix} 0.8750 \\ 0.7999 \\ 0.7425 \\ 0.7425 \end{pmatrix}$$

In this case the maximal eigenvalue, $\|\lambda\| = 0.8750$ is less than 1, so \bar{X}_0 is locally asymptotically stable; it is not sensitive to initial conditions.

The following sensitivity analysis was done for the harvest rates of the system. The preliminary analysis was done with each of the harvest rates set to 0. Each harvest rate then increased by a step size of 0.01 until it becomes within 0.01 of the

survival rate of the respective sub-age class. For example, the harvest rate for Second Year Males (h_{sm}) starts at 0 and then increases by 0.01 until it is within 0.01 of the survival rate for Second Year Males, (s_{sm}). At that point, the harvest rate stops growing. This does not mean that the growth in the other harvest rates also stops - the rates examined in the numerical simulation will increase until they are within 0.01 of the survival rate. The restrictions on the growth of the harvest rates ensures that there are two steady state solutions based on the aforementioned criteria.

In the following analysis all harvest rates are under consideration; the rate for each age/gender class starts at zero and increases. The harvest rate for Cubs remains zero at all times because it is illegal to harvest Cubs. The harvest for Third Year females and Adult females also increases - this may, however, be inaccurate, as the harvesting of a mother with Cubs is also protected against by law.

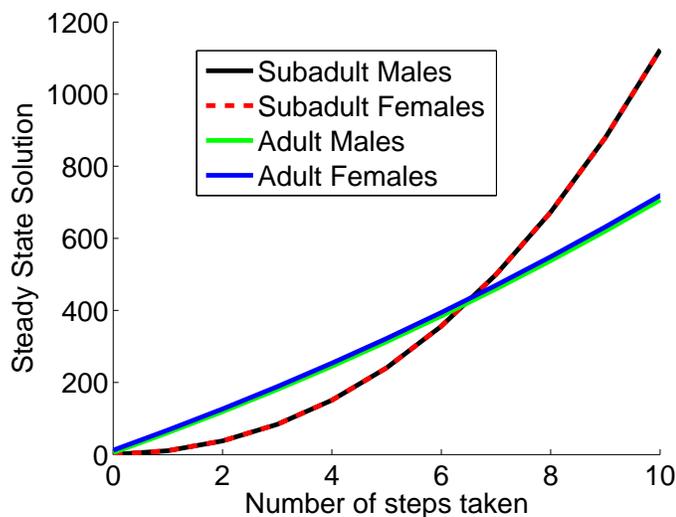


Figure 2.2: Steady State Solutions with varying harvest

Figure 2.2 shows the different steady state solutions as the harvest rates change. The number of steps taken corresponds to the number of times the harvest rates increase by the given step size. Only the first ten years are examined because, after this point in time the steady state solutions for all independent variables reach extremely high numbers.

Figure 2.3 shows the eigenvalues for the nonzero steady state solution (shown in Figure 2.2). All imaginary parts are ignored in terms of the graph. As can be seen, even if every harvest rate is set to zero, the principle eigenvalue is greater than one. Additionally, $\|\lambda\| > 1$ for all harvest rates examined.

Figure 2.4 shows the eigenvalues for the zero steady state solution. The principle eigenvalue is always between 0 and 1, though the it becomes very close to one when

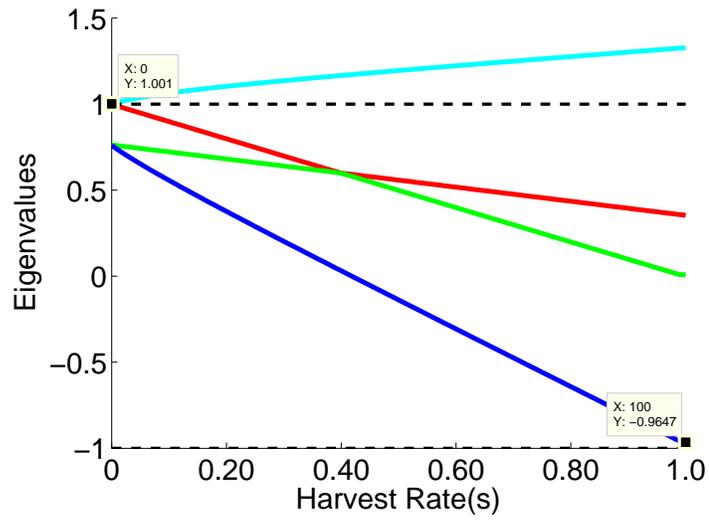


Figure 2.3: Eigenvalues for Nonzero Steady State Solutions

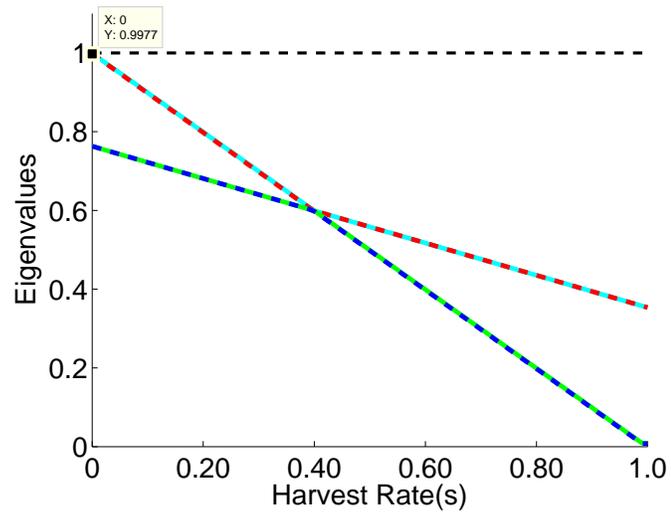


Figure 2.4: Eigenvalues for Zero Solution

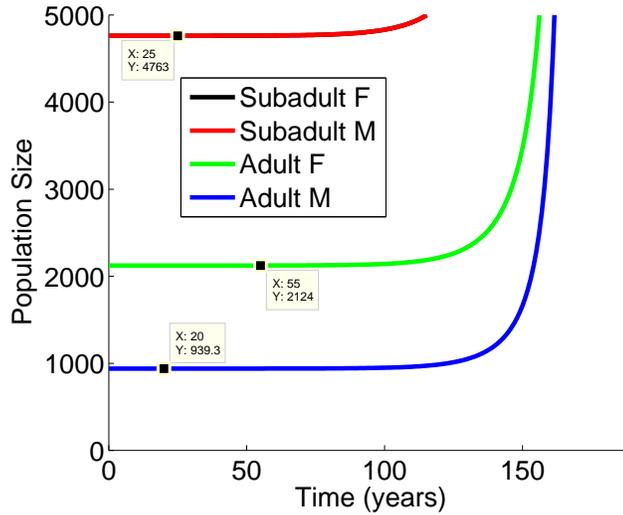


Figure 2.5: Population with initial condition \bar{X}_1 , Harvest as in Appendix A.5

the harvest rates are equal to zero. This suggests that when the harvest rates are 0, if the initial population sizes are within some arbitrarily small ϵ of the zero solution the Black Bear population will limit towards the zero solution.

2.3.4 Simulations

The rounding error from the Matlab prevents a simulation which shows the steady state solution found in Section 2.3.3. A simulation using \bar{X}_1 shows that after F is applied once, the solutions do not change significantly. The growth away from \bar{X}_1 is extremely small at first. In fact, upon examining Figure 2.5, it is shown that iterating F fifty five times does not map \bar{X}_1 significantly away from itself. The population does explode to infinity beginning at approximately year 150. Looking at a solution slightly below \bar{X}_1 shows the same behavior. It is not guaranteed that all initial conditions $< \bar{X}_1$ limit towards the zero solution - in fact, such an initial condition can still explode towards infinity in finite time. At this point, nothing can be said concerning the basin of attraction for \bar{X}_0 .

Let us investigate the overall behavior of the system. The following tables have the survival and harvest rates parameters used in the simulations of the Basic Model Version 1.

The break down of the sub-age classes (the v_{xy} terms) are in Table 2.2.

What follows is a simulation with the following harvest and survival rates, obtained directly from the literature [2]. The first simulation is done with an initial population size of 9500 bears divided amongst the four Age classes arbitrarily -

$$[S_{m,0}, S_{f,0}, A_{m,0}, A_{f,0}] = [2937.5, 2937.5, 1812.5, 1812.5].$$

Parameter	Units	Value	Source
s_c - Cub survival	percentage	0.80	VDGIF [5]
s_{ff} - First Year female survival	percentage	0.85	estimate
s_{fm} - First Year male survival	percentage	0.85	estimate
s_{sf} - Second Year female survival	percentage	0.995	[2]
s_{sm} - Second Year male survival	percentage	0.999	[2]
s_{tf} - Third Year female survival	percentage	0.995	[2]
s_{tm} - Third Year male survival	percentage	0.999	[2]
s_{af} - female survival over three years of age	percentage	0.998	Klenzendorf, Sybille [2]
s_{am} - male survival over three years of age	percentage	0.999	[2]
h_c - Cub harvesting	percentage	0	[2]
h_{ff} - First Year female harvest	percentage	0.05	estimate
h_{fm} - First Year male harvest	percentage	0.05	estimate
h_{sf} - Second Year female harvest	percentage	0.22	[2]
h_{sm} - Second Year male harvest	percentage	0.45	[2]
h_{tf} - Third Year female harvest	percentage	0.05	[2]
h_{tm} - Third Year male harvest	percentage	0.30	[2]
h_{af} - Adult female harvest	percentage	0.13	[2]
h_{am} - Adult male harvest	percentage	0.19	[2]

Table 2.1: Survival and Harvest rates for sub-age classes

Parameter	Units	Value
v_{cm} - the proportion of Cubs in $S_{m,t}$	percentage	0.5185
v_{fm} - the proportion of First Years in $S_{m,t}$	percentage	0.4096
v_{sm} - the proportion of Second Years in $S_{m,t}$	percentage	0.0719
v_{cf} - the proportion of Cubs in $S_{f,t}$	percentage	0.5186
v_{ff} - the proportion of First Years in $S_{f,t}$	percentage	0.4096
v_{sf} - the proportion of Second Years in $S_{f,t}$	percentage	0.0719
v_{tm} - the proportion of Third Years in $A_{m,t}$	percentage	0.083
v_{am} - the proportion of bears over the age of three in $A_{m,t}$	percentage	0.9170
v_{tf} - the proportion of Third Years in $A_{f,t}$	percentage	0.0909
v_{af} - the proportion of bears over the age of three in $A_{f,t}$	percentage	0.9091

Table 2.2: Sub-age class proportions

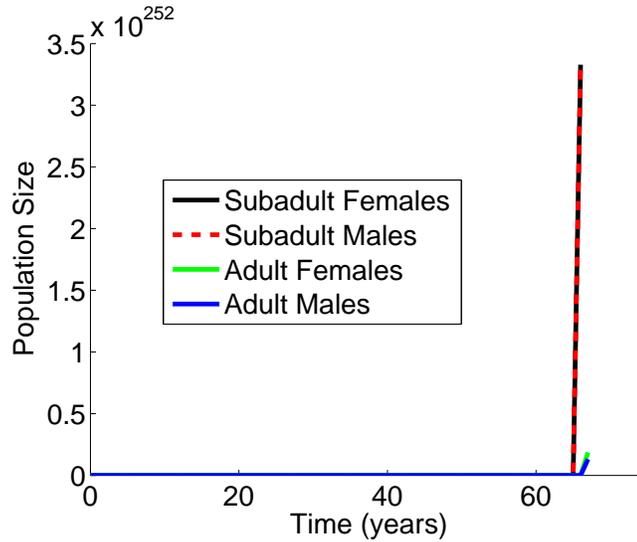


Figure 2.6: Population Break Down, Harvest as in Appendix A.5, Initial total 9500 bears

Figure 2.6 shows a breakdown of the four Age Classes with parameters mentioned above. Little remains to expand upon, other than the population's explosion in finite time. As the Black Bear population size deviates from the initial condition, the validity of the results yielded by the simulation becomes weaker because there is no carrying capacity term in the equations and, as the population becomes larger than approximately 75% of the carrying capacity, density dependent effects should come in to play [7]. It is interesting that Figure 2.8 shows the females reaching a higher percentage of the total Black Bear population before the population tends towards infinity.

Figure 2.8 which shows the proportion of males and females in the total population. The male percentage is given by

$$\frac{S_{m,t} + A_{m,t}}{S_{m,t} + A_{m,t} + S_{f,t} + A_{f,t}}.$$

and the female percentage is given by 1 less the male percentage. Any initial condition larger than 9500 Black Bears will result in the similar dynamics given the same harvest and survival rates, except for the nonzero steady state solution mentioned earlier. Let us examine the dynamics of the system as the initial population size is less than 9500 bears.

Based on simulations, it appears that any initial total population less than or equal to 9041 bears (which corresponds to $[S_{m,0}, S_{f,0}, A_{m,0}, A_{f,0}] = [1724.9, 1724.9, 2795.6, 2795.6]$) causes the population to tend towards extinction. This is entirely dependent on the manner in which the initial population is distributed amongst the age classes. As such, this information does not give a complete picture

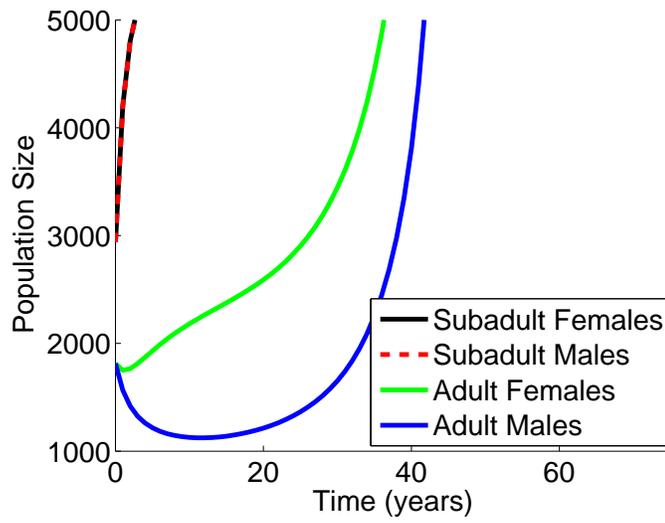


Figure 2.7: Population Break Down, Harvest as in Appendix A.5, Initial total 9500 bears

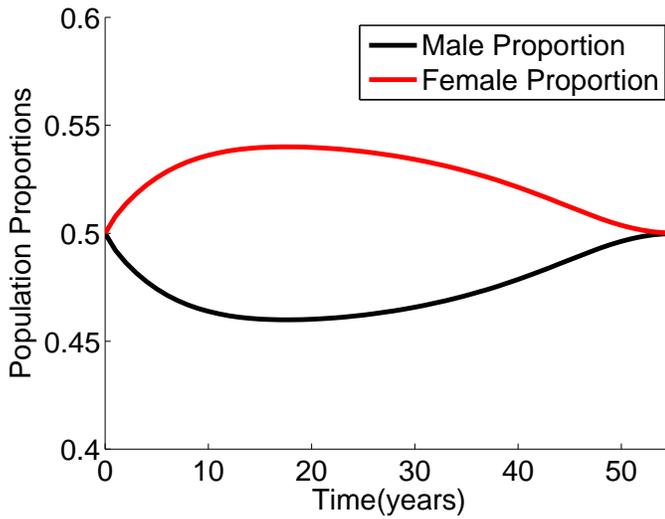


Figure 2.8: Population Proportions, Harvest as in Appendix A.5, Initial total 9500 bears

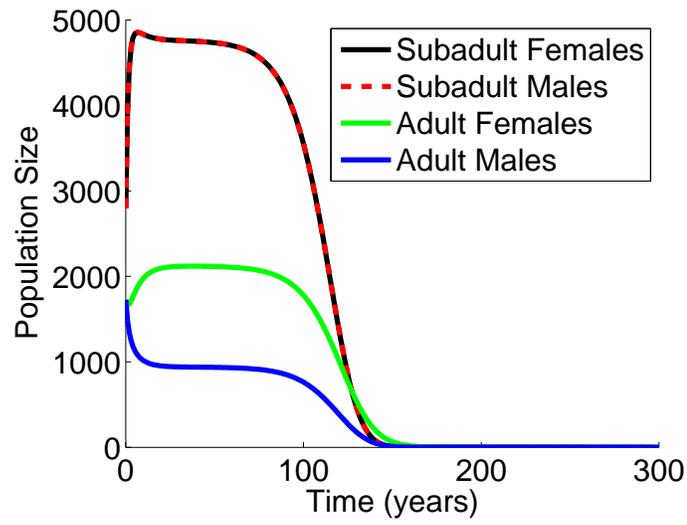


Figure 2.9: Population Breakdown, Harvest as in Appendix A.5, Initial total 9041 bears

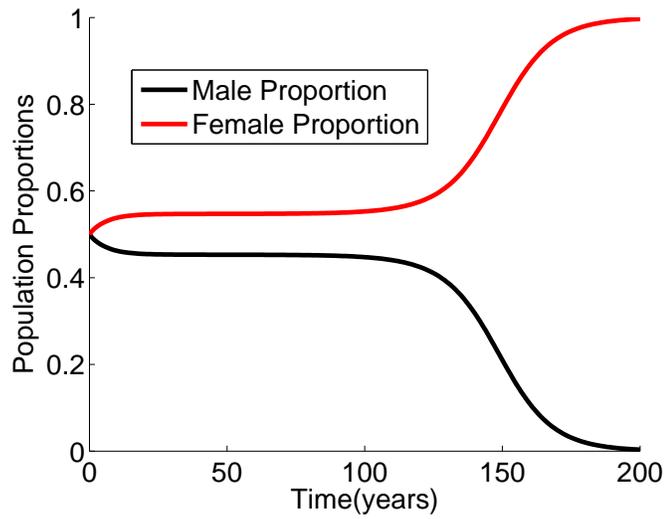


Figure 2.10: Population Proportions, Harvest as in Appendix A.5, Initial total 9041 bears

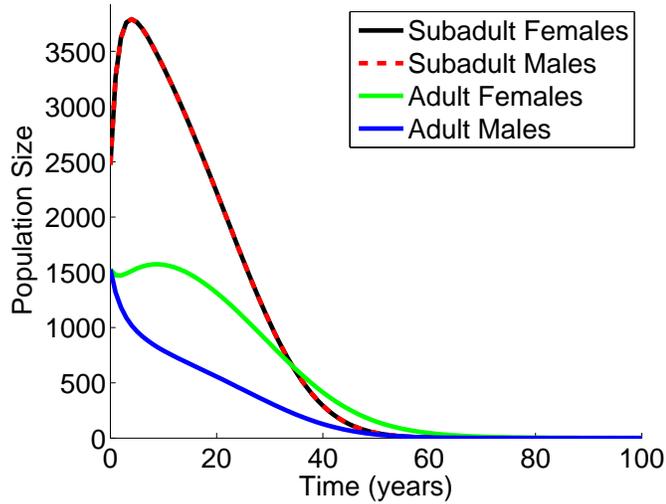


Figure 2.11: Population Break Down, Harvest as in Appendix A.5, Initial total 8,000 bears

of the basin of attraction around \bar{X}_0 ; it does indicate a basin of attraction for all initial conditions up to (and equal to) 9041 bears based on the division scheme of the Matlab code, which is arbitrary. This result implies that any initial condition, $[S_{m,0}, S_{f,0}, A_{m,0}, A_{f,0}] \leq [1724.9, 1724.9, 2795.6, 2795.6]$ will limit towards the zero solution.

Figure 2.9 is particularly interesting due to the behavior of the system of difference equations as the Black Bear population tends towards extinction. Notice that all populations experience growth except for the Adult male ($A_{f,t}$) population. The population sizes then show a period of relative stability (though they are still in decline) - when the solution sizes are near \bar{X}_1 (Section 2.3.3). In approximately year 90 the populations decline rapidly towards extinction. For initial conditions less than 9041 bears, the period of stability noted in Figure 2.9 disappears (as can be seen in Figure 2.11).

Of particular interest is the exact cause of the decline of the population. The behavior seen in Figure 2.9 does not expressly suggest that the decline in population is tied directly to either the male or the female population. The Adult Male population, which affects the number of Cubs born per year, decreases initially which could explain the decline in growth of the other populations. Examining Figure 2.10, we see that the proportion of females in the population eventually reaches 100% as the male population declines.

A simulation with a population size of 8,000 can be seen in Figure 2.11. The behavior seen in the simulation has changed. There exists no period of time where the

h_c - Cub harvesting	percentage	0
h_{ff} - First Year female harvest	percentage	0.0537
h_{fm} - First Year male harvest	percentage	0.0537
h_{sf} - Second Year female harvest	percentage	0.2363
h_{sm} - Second Year male harvest	percentage	0.4833
h_{tf} - Third Year female harvest	percentage	0.0537
h_{tm} - Third Year male harvest	percentage	0.3222
h_{af} - Adult female harvest	percentage	0.1396
h_{am} - Adult male harvest	percentage	0.2041

Table 2.3: Harvest after 2 years of growth at 7.4% per year

rate of decline is approximately zero, as was encountered in the simulation depicted in Figure 2.9. The Subadult male, Subadult female, and Adult female populations all experience growth; the Adult male population experiences decline following the first iteration of F . Figure 2.11 shows stronger evidence that the decline of the male population (in this case, the Adult Male population) causes the extinction of the bear population.

Let us now go back to an initial population size of 9,500 bears. With the parameter values from Table 2.1 the population explodes towards infinity. Assume that the harvest rate can change each year, and that the harvest of each sub-age category increases by 7.4% (mentioned in [6]) each year. The increase of 7.4% per year in harvest is somewhat arbitrary. There is some basis for this figure in the literature; however the 7.4% increase refers to the total number of bears harvested, not the harvest rates. The use of that percentage as a step size in the harvest rate does allow us to compare year 0 in the model to the year 2002, in which the harvest rate data was collected in [2].

Simulations reveal that it takes two years of increased harvest at 7.4% increase per year to cause the population to tend towards extinction with an initial population size of 9500 bears. After two years of growth, the harvest rates of the sub-age classes are found in Table 2.3.

Refer to Figure 2.12 for a breakdown of the Age classes after 2 years of harvest growth. The total population grows for the first 6 years (roughly corresponding to years 2002-2008) and then reaches extinction in year 91 (roughly year 2095). The growth experienced in the first 6 years agrees with the current literature [2] which speculates that there is growth in the Black Bear population based on population estimates from 2002.

The number of years in growth required to cause the population to tend towards extinction depends on the initial population size. For example, with an initial popu-

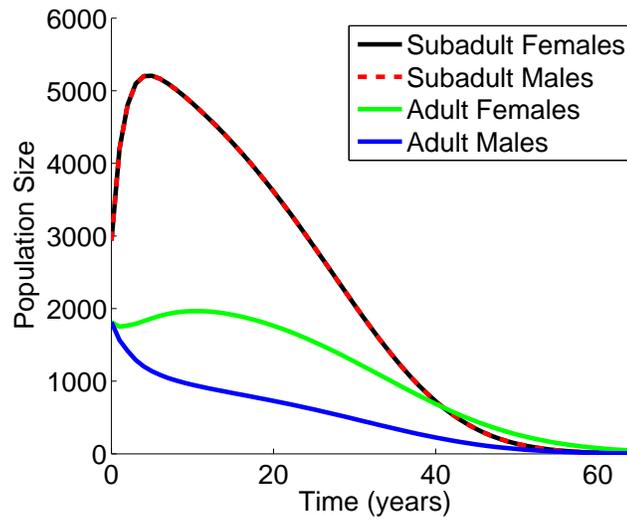


Figure 2.12: Population Break Down following 2 years of harvest growth

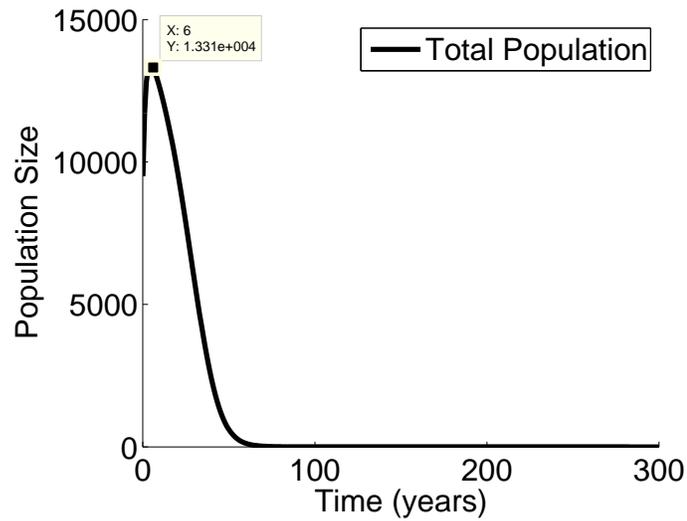


Figure 2.13: Total Population after 2 years of harvest growth

lation of 15,000, it requires 6 years of harvest growth to cause the population to limit towards the zero solution. Additionally, with an initial condition of 50,000 bears, no amount of harvest will cause the population to tend towards extinction. Though this initial condition is not realistic, this still demonstrates that the initial condition affects the long term preservation of the species. The quadratic birth term most likely causes the sensitivity towards different initial conditions. The product $b * A_{f,t} * A_{m,t}$, which yields part the birth term in the Subadult equations, grows rapidly for all but relatively small initial conditions ($A_{f,0}, A_{m,0} \leq (1,000, 1,000)$). As $A_{f,t}$ and/or $A_{m,t} \rightarrow \infty$, $b * A_{f,t} * A_{m,t} \rightarrow \infty$, and the higher the harvest rate needed to negate the new bears born into the population.

In particular, examine the harvest rate of the Second Year Males (which are part of the Subadult males). After two years of growth, $h_{sm} = 0.4833$ implying that hunters harvest approximately 50% of the Second Year males (part of the Subadult male population) per year after two years. Recall, however, that only the proportion $v_{sm} = 0.0719$ of the Subadult males are Second Year males. The second largest harvest rate is for the Third Year males (part of the Adult male population) in which approximately 32% of the population is harvested per year after two years of growth in harvest. It should be considered that the shortage of males in the Black Bear population causes the extinction of the population.

If we consider a model in which only a females are tracked (and thus, we assume that the number of males is roughly equivalent to the number of females - something which already differs from the current simulations) would we expect the population to tend towards extinction given the same initial conditions and harvest rates? We can easily alter the equations (discussed in Section 2.3.2 of the basic model) to only include females by altering the birth term to have $A_{f,t}^2$ instead of $A_{f,t} * A_{m,t}$.

$$S_{f,t+1} = 0.5 * p_f * b_t * \beta_1 * v_{tf} * \underbrace{A_{f,t}^2}_{\text{new birth term}} + 0.5 * p_f * b_a * \beta_2 * v_{af} * A_{f,t} * A_{m,t} \\ + (s_{cf} - h_{cf}) * v_{cf} * S_{f,t} + (s_{ff} - h_{ff}) * v_{ff} * S_{f,t} - (s_{sf} - h_{sf}) * v_{sf} * S_{f,t}.$$

The Adult Female equation remains unchanged:

$$A_{f,t+1} = (s_{sf} - h_{sf}) * v_{sf} * S_{f,t} + (s_{tf} - h_{tf}) * v_{tf} * A_{f,t} \\ + (s_{af} - h_{af}) * v_{af} * A_{f,t}.$$

With this system of equations it requires 8 years of the 7.4% increase in harvest to cause the population to tend towards extinction, using an initial population size

of 9500. This analysis in and of itself does not lend itself to the argument that males are inherently more important than females in terms of preserving the species, or in terms of the elasticity of the parameters. It does suggest that a model which only takes into account the female population lacks an essential dynamic to the modeling of this population.

2.4 Basic Model Version 2

In order to better comment on policy questions concerning the harvest of the Black Bear population, the Basic Model Version 2 replaces the harvest rates with constant harvest terms. It will be assumed that hunters can only harvest a constant number of bears from the population. Additionally, a density dependent survival term will be incorporated into the equations in order to provide a carrying capacity to prevent the population from exploding towards infinity in finite time. In order to do this, a method for examining the density of bears in relation to space needs to be implemented. Any assumptions encountered for the first version of the Basic Model (Section 2.3.1) also apply to this model unless otherwise specified in the following Sections. Specifically, those terms that change deal with a weighted survival term, and a constant harvest.

2.4.1 Territories

Though space is not explicitly accounted for in the basic model, the number of territories available for bears still serve as something of a spatial element for both the Basic Model Version 2 and the Extended Model. A territory is defined as the amount of space that a bear occupies in a given day - the size of a territory can vary based on the amount of food available for the bears. In this case we are not distinguishing between territory size differences between the age and gender classes. A territory should not be confused with a home range - defined as the maximal territory that a bear might cover. For example an Adult male bear has a home range of up to 173 kilometers², while an Adult female bear has a home range of up to 41 kilometers² [2]. A home range can be thought of as a bear's maximal territory size, which fluctuates based on availability of food. Let us assume that there are x number of territories available in a given location. Many terms in the model incorporate population density with regard to the number of territories available. The values in Dr. Klenzendorf's thesis are taken and used in functions designed to scale them based on the density of the Black Bear population.

Let us assume that there are 10,000 territories available for bears to inhabit. Additionally, let us assume that in general, that x territories can sustain some additional bears given by a proportion, p , of the territories x . So, 10,000 territories will be able to sustain more than 10,000 bears, because it is assumed that bear does not occupy all of its territory at one particular moment, giving other bears a chance to scavenge. The logic is that, even though a bear might have a territory of 10 kilometers² (as an example), the bear will not be everywhere on that territory at once. Thus, a bear could have Roaming status - where it has no territory of its own, but can still survive an the are due to surplus food. Cubs are not counted as part of the total population because they remain with their mothers [4]. From this point forward, 10,000 bears will be referred to as the saturation point of the population because as the population exceeds 10,000 bears there are mechanisms in place which decrease the survivability of the bear population. These are discussed in the next section.

2.4.2 Weighted Survival

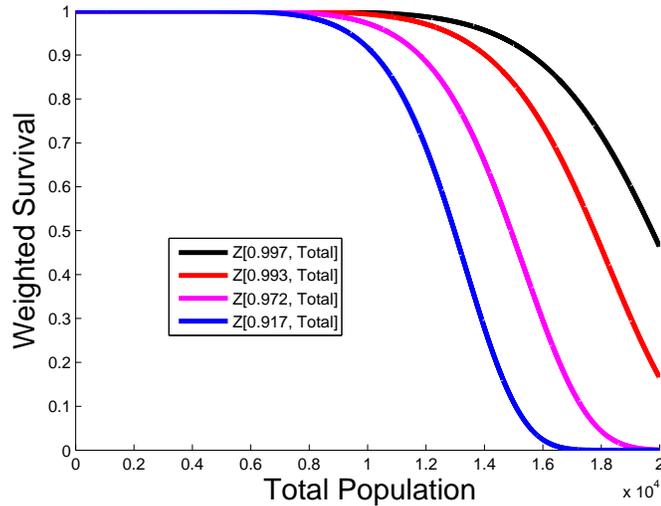
The first function examined scales the survival rate of the Black Bear population based on the territory cap. As a population grows denser and denser, the food supply becomes limited. We are assuming that there is enough food to sustain 10,000 bears (which is considered the saturated total population size) after which point there starts to be competition for resources. The weighted function will need to reflect this dynamic. Assume x is the total population size.

The weighted survival function will be denoted as Z . There is a distinct Z value for each age/gender category in the model. The saturation point mentioned is a total population size of 10,000 bears. The saturated survival rate is the survival rate from the literature, and it occurs exactly at the saturation point of the population. In this case, the saturated survival directly corresponds to the survival rates encountered in Dr. Klenzendorf's thesis [2]. It is assumed that the survival rates provided by Dr. Klenzendorf occur at a saturated population size, where bears are not competing for resources. This seems to agree with her postulation that the Black Bear population at her study site was experiencing growth [2]. To summarize,

$$\text{As } x \rightarrow \infty, f(x) \rightarrow 0$$

$$\text{As } x \rightarrow 0, f(x) \rightarrow 1$$

$$\text{As } x \rightarrow \text{the saturation point}, f(x) \rightarrow \text{saturated survival rate.}$$



Where the saturation point is 10,000 bears, and the saturated survival rate a value encountered in [2], mentioned in Section 2.3.4, Table 2.2.

Consider the following equation:

$$Z[\text{saturated survival}, Total_t] = \text{saturated survival} * e^{(\ln(\text{saturated survival}) * ((\frac{Total_t}{10,000})^8 - 1))}$$

Where $Total_t$ are the total number of bears at time t . The saturated survival is obtained directly from the constant survival rates found in [2]. $Total_t$ updates dynamically. The number 10,000 in the denominator of the exponent reflects the territory cap on the population. Note the term, $(\frac{Total_t}{10,000})^8$. It is raised to the 8th power in order to ensure that, as the population grows to be larger than 10,000 bears, then the survivability declines rapidly.

The following graph uses a variety of saturated survivals:

As the population reaches 10,000, the weighted survival approaches the saturated survival rate of 99.7%. Anything below the saturated population results in an increase in survivability, justifiable, perhaps, by an overabundance of food resulting from the low number of bears or less competition. Each sub-age class excluding Cubs (First Years, Second Years, Third Years, etc.) has its own weighted survival, based on the values found in [2], shown in Section 2.3.4, Table 2.2. It is also in the Appendix, A.5.

Not all weighted survival functions have exactly the same behavior. Reference Figure 2.4.2. This displays the behavior of the weighted harvest function with varying saturated harvest values. In general, the closer the saturated survival rate is to 1, the longer it takes for the function to limit towards 0. The lower the saturated survival, the quicker that the function limits to zero. As the saturated survival limits towards

zero, the weighted survival will approach zero more rapidly. What this implies is that bears with a lower saturated survival will be more affected by the change in total population in that the weighted survival will reach 0 more rapidly than those bears with a higher saturated survival. It is the general trend in the survival rates of the Black Bears [2] that older bears have a higher survivability than younger bears, which might have allowed for a biological justification of this method of weighting. Notice that there is a distinct Z for every single sub-age class within the model except for Cubs - this includes First Years, Second Years, Third Years, and bears older than three. Cubs are excluded because birth is assumed to occur only in females that have territory and resources to support young. Because the weighted survival will affect the breeding females, this will indirectly alter the number of Cubs born each year.

2.4.3 Equations

The equations will have the form:

$$\begin{aligned} \text{Subadult females} = & \max(0, \text{females born} + \text{survival of female Cubs} \\ & + \text{survival of First Year females} - \text{harvest}) \end{aligned}$$

$$\begin{aligned} \text{Subadult males} = & \max(0, \text{males born} + \text{survival of male Cubs} \\ & + \text{survival of First Year males} - \text{harvest}) \end{aligned}$$

$$\begin{aligned} \text{Adult females} = & \max(0, \text{Second Year females which mature} + \text{survival of Third} \\ & \text{Year females} + \text{survival of older females} - \text{harvest}) \end{aligned}$$

$$\begin{aligned} \text{Adult males} = & \max(0, \text{Second Year males which mature} + \text{survival of Third} \\ & \text{Year females} + \text{survival of older males} - \text{harvest}) \end{aligned}$$

The equations for males and females are identical in form, though each has distinct parameters. The following equations will only be shown for the female bears; the corresponding male equations can be found in the Appendix, A.3.

$$\begin{aligned} S_{f,t+1} = & \max\{0, 0.5 * p_f * b_t * v_{tf} * A_{f,t} * A_{m,t} * \beta + \\ & 0.5 * p_f * b_a * A_{f,t} * A_{m,t} * \beta + (s_{cf}) * v_{cf} * S_{f,t} + \\ & (Z[s_{ff}, Total_t]) * v_{ff} * S_{f,t} - h_1\} \end{aligned}$$

*Recall that the Cubs are not subject to a weighted survival rate: Section 2.4.2.

Where

$S_{f,t}$ —Subadult female Bears at time t .

p_f —The proportion of females that breed in any given year.

b_t —The birthrate of Third Year females.

$A_{m,t}$ —Adult male Bears at time t . This category includes any male bear which is three years of age, or older.

$A_{f,t}$ —Adult female Bears at time t . This category includes any female bear which is three years of age, or older.

v_{xy} —The proportion of age class x , and gender y . Recall that Cubs, First Year Bears, and Second Year Bears are considered Subadults.

$x \in \{\text{Cubs}(c), \text{First Year Bears}(f), \text{Second Year Bears}(s),$
Third Year Bears(t), Adults(a)\},

$y \in \{\text{males}(m), \text{females}(f)\}$.

b_a —The birthrate of female bears above the age of three.

s_{xy} —The saturated survival rate of age class x and gender y ,
where x and y are defined as above.

h_i —The harvest constant of age class $i \in$

\{\text{Subadult males (1), Subadult females (2), Adult males (3),
Adult females(4)}\}

$Z[s_{xy}, Total_t]$ —The weighted survival function, with x, y defined as above.

This is derived in Section 2.4.2.

The Adult equation is as follows,

$$\begin{aligned}
A_{f,t+1} = \max\{ & 0, (Z[s_{sf}, Total_t]) * v_{sf} * S_{f,t} + \\
& (Z[s_{tf}, Total_t]) * v_{af} * A_{f,t} + \\
& (Z[s_{af}, Total_t]) * A_{f,t} - h_4 \}
\end{aligned}$$

All terms are defined as above.

2.4.4 Analysis and Simulations

The feasibility of finding a nonzero steady state solution given the complexity of the weighted survival term by hand is low. With the equations for the second version of the Basic Model it is impossible to ensure that

$$F : \Omega \rightarrow \Omega$$

where $\Omega = \{(S_m, S_f, A_m, A_f) \mid S_m, S_f, A_m, A_f \geq 0\}$. The Matlab code is designed so that any negative population size is reset to 0. Though the simulations will be geared towards finding a steady state solution (should any non-zero steady state solution exist), the real aim of this particular model is to answer an important policy question through examining various harvesting constants.

As a reminder, the proportions in the population (v_{xy}) are the same as those used in the first version of the basic model - Section 2.3.4, Table 2.2, Appendix A.5.

For the first simulation, all harvest constants are set to zero in order to examine the distribution of the bear population. Figure 2.14 shows that the population exhibits what appears to be periodic behavior with the Subadult males and females alternating between an approximate size of 7080 and 4392. The Adult males alternate between approximately 3592 and 4325 bears; the Adult females alternate between 920.2 and 1694. This results in a Total population size which alternates between 14,000 and 20,000. This isn't completely unreasonable given a soft cap of 10,000 bears on the population. If this is indeed a periodic solution, for 0 harvest it appears to be unstable.

It is interesting to notice that a period of growth in the Subadult males and females follows a period of growth in both Adult males and females. Additionally, the period of decline in Subadult males and females follows the period of decline in the Adult males and females. This is as expected based on the nature of new births entering the population - if there are more adults in the previous time period, there will be more births.

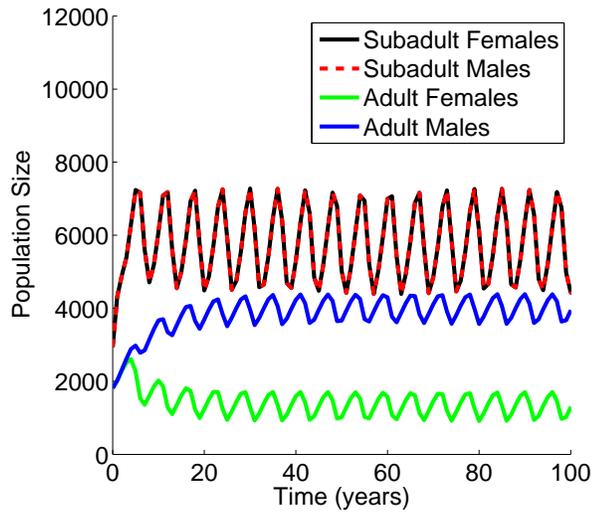


Figure 2.14: Population Break Down, 0 Harvest, Initial total 9500 bears

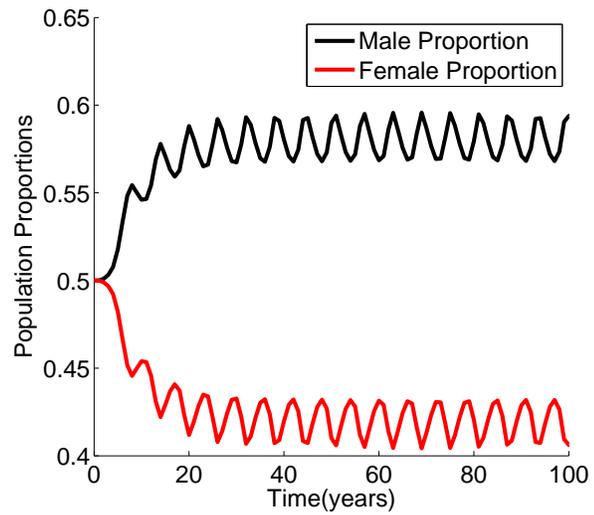


Figure 2.15: Population Proportions, 0 Harvest, Initial total 9500 bears

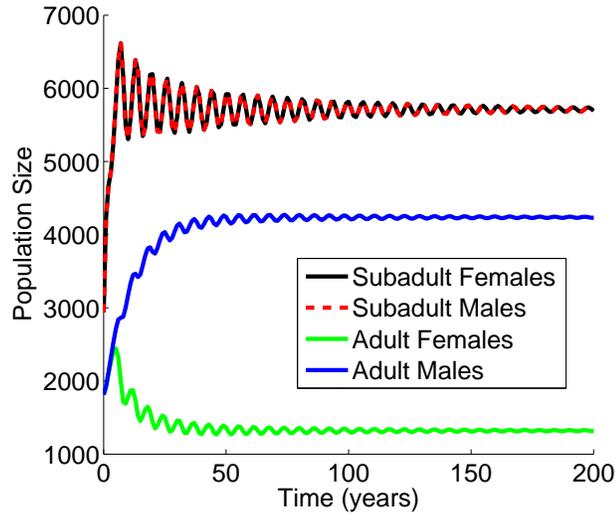


Figure 2.16: Population Break Down, 100 Harvest, Initial total 9500 bears

The proportion of males to females in the population can be seen in Figure 2.15. The male proportion stays between approximately 55% and 60% of the population, which leaves the females between 40% and 45%. This does not completely agree with the literature - the expected and observed values in [2] placed the proportion of males to females at 0.3:1 and 0.6:1 respectively. This may have to do with special environmental conditions of the study area used by Klenzendorf. Various runs of different initial conditions reveal that the solutions always behave as in Figure 2.14, though for smaller initial conditions it takes a longer period of time for the populations to enter their apparent orbits. For example, a population size of only 10 bears takes over 1,000 years to enter its apparent orbit.

The next natural question has to do with the amount of harvesting necessary to cause the population to go towards extinction. In order for there to be sufficient time for the population to stabilize after the initial condition, the constant harvest rate will not be applied until after five iterations of the map. The initial harvest will be 100 bears per year.

The effect of harvesting 100 bears per year has a damping effect on the oscillations seen in Figure 2.14. Refer to Figure 2.16 and 2.17 for the Population Break Down and the Gender Proportions respectively. Now, the total population limits towards ≈ 16980 bears, with Subadult males and females at 5712 bears each, Adult males at 4237, and 1321.

The problem with using these homogenized harvest constants has to do with the inability of the terms to distinguish between those bears protected by Virginia Law, and it does not reflect the hunter preference for larger bears. The VDGIF states that

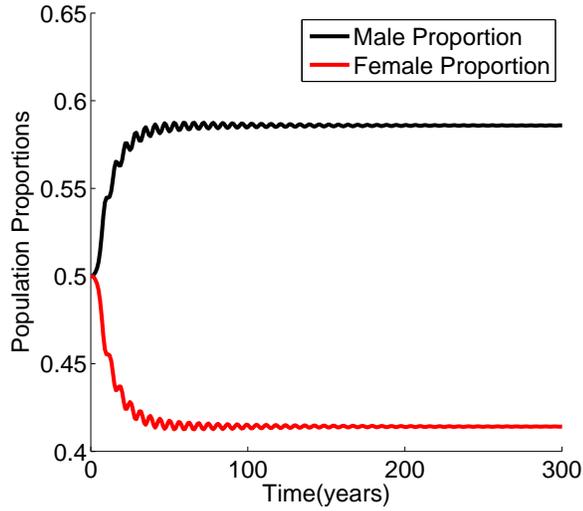


Figure 2.17: Population Proportions, 100 Harvest, Initial total 9500 bears

in 2009 over 40% of the bears harvested were females, up from a 5 year average of 37% [6]. For sake of ease, assume that 40% of all harvested bears are female. Because it can be supposed that larger bears are preferred by hunters for trophies, the majority of the harvest would most likely occur in the Second Year, Third Year, and Adult sub-age classes. Cub harvest would be nonexistent under Virginia Legislature [2]. Let us assume that 40% of male/female harvest occurs in the Subadult category, and the remainder occurs in the Adult category. So,

$$\text{Subadult male harvest} = h_1 = 0.60 * 0.40 * \text{Total Harvested}$$

$$\text{Subadult female harvest} = h_2 = 0.40 * 0.40 * \text{Total Harvested}$$

$$\text{Adult male harvest} = h_3 = 0.60 * 0.60 * \text{Total Harvested}$$

$$\text{Adult female harvest} = h_4 = 0.40 * 0.60 * \text{Total Harvested}.$$

These next simulations are run assuming a total harvest of 1,387 bears - a sum of numbers given by the VDGIF as the number of bears harvested in select counties in Virginia [6]. Then,

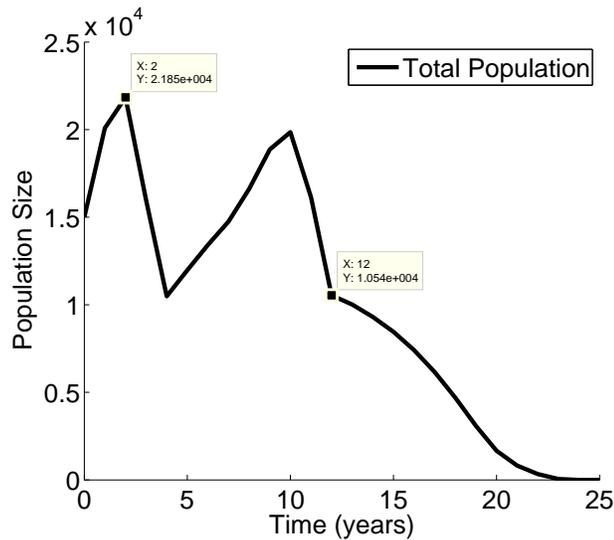


Figure 2.18: Total Population, Pooled Harvest 1,387, Initial total 15,000 bears

$$h_1 = 0.60 * 0.40 * \text{Total Harvested} \approx 332.88$$

$$h_2 = 0.40 * 0.40 * \text{Total Harvested} \approx 221.92$$

$$h_3 = 0.60 * 0.60 * \text{Total Harvested} \approx 499.32$$

$$h_4 = 0.40 * 0.60 * \text{Total Harvested} \approx 332.880.$$

Using these harvest constants is enough to cause the population to go towards extinction. Refer to Figure 2.18 and Figure 2.19 given an initial population size of 15,000. Given that the supposed periodic solution is not sensitive to initial conditions, one can surmise that the population will tend towards extinction for all initial conditions. For what total harvest will the population persist, given an initial condition of 15,000 bears?

Simulations reveal that a total harvest as low as 870 bears will cause the population to tend towards extinction, given an initial condition of 15,000 bears. Undoubtedly, with lower initial conditions it will take less harvest in order to cause the population to go towards extinction, due to the longer amount of time it takes for the population to reach its orbit. Though, with an initial population of 5,000 bears, it still takes a total harvest of 870 to cause the population to go towards extinction. For an initial population of 1,000 bears, a total harvest of only 88 bears causes the population to go towards extinction. This does not suggest that smaller populations are very resilient to the effects of harvesting. However, it should be noted that at small population sizes, the use of a constant instead of a rate weakens the conclusions that can be drawn

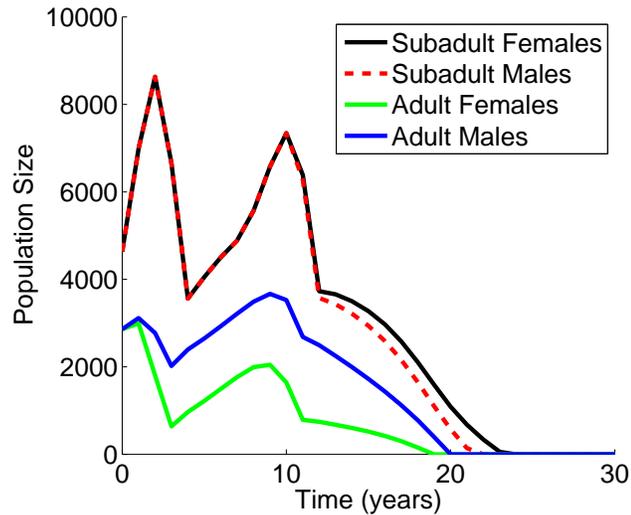


Figure 2.19: Population Breakdown

from the simulation. These simulations should give a reasonable idea for what will occur at higher population levels, when the Black Bear population is near carrying capacity.

2.5 Ending Remarks

Though the first version of the basic model is reasonably easy to analyze by hand and through simulations, there are many assumptions (especially concerning density dependent effects) which greatly limit the analysis yielded by the model for larger population sizes, and for initial conditions which cause the population to explode within finite time. In these cases, the bear population would no longer be less than 75% of a carrying capacity [7], and would violate one of the assumptions used in the formation of this model. However, this model gives the best intuition for small population sizes.

The second version of the Basic Model aims to relax some assumptions in the first version of the Basic Model. By doing so, it made analyzing the model by hand extremely difficult. In terms of simulations for the second version of the Basic Model, only cursory remarks can be made concerning steady state solutions or periodic orbits without utilizing more complex analytical tools. Additionally, as the Black Bear population size gets smaller, the validity and generalizability of the results weakens.

The extended version of the model expands all sub-age classes mentioned in the Basic Model in order to better model the effects of harvesting on distinct age classes. The weighted survival term remains, and a new weighted harvest rate is implemented

in lieu of a harvest constant in order to make more accurate statements when the total population of the Black Bears is small. Finally, a new birth term is implemented in order to relax the assumptions imposed by the birth term $(A_f * A_m)$ used in both versions of the Basic Model.

Chapter 3

The Extended Model

3.1 Population Dynamics

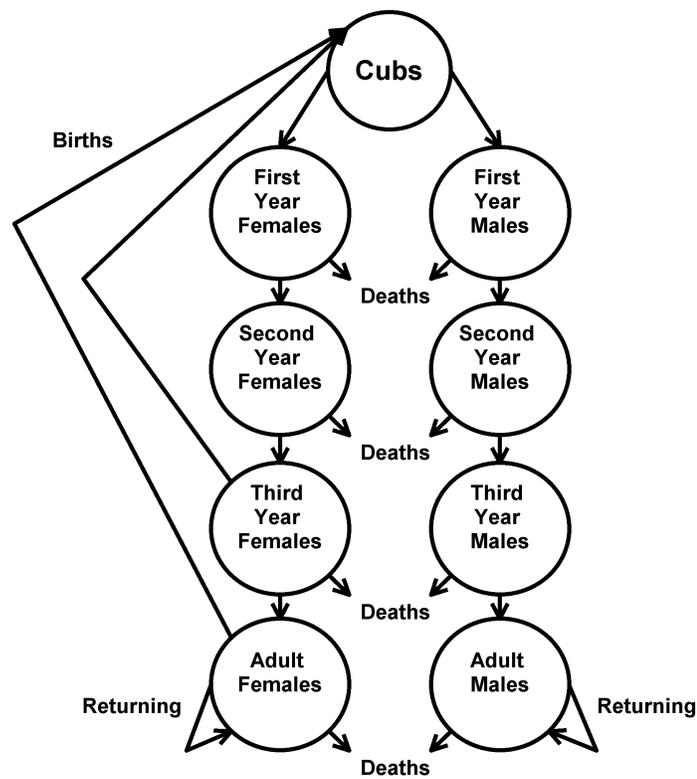


Figure 3.1: Flowchart for the Black Bear population in the extended model

Fig. 3.1 gives an overview of the way the population is broken down. In this model we have distinct stages of life, rather than the compressed life stages presented in the Basic Model. In the Basic Model we looked at Subadults as including Cubs, First Year bears, and Second Year bears. Similarly, Adults included Third Year Bears and older bears. In this model, all of the age classifications which were previously condensed into four equations are now expanded. Note that Cubs are not distinguished by gender. After one year the Cubs become First Year bears, which are distinguished

by gender. In the chart below, it should be noted that the Adult Male and Adult Female age classes are broken down into 16 distinct subclasses, shown in Fig. 3.2.

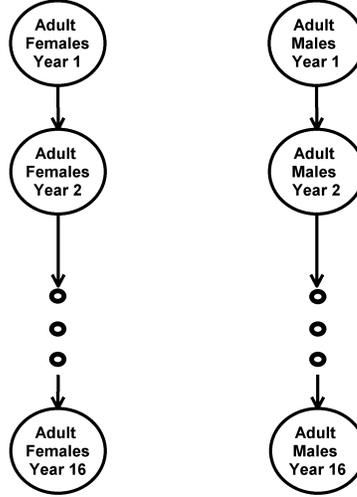


Figure 3.2: Flowchart breaking down the Adult populations.

Splitting the Adult populations into subpopulations is necessary in order to keep track of an accurate breeding population which excludes bears too old to breed. Additionally, the split allows for distinct harvesting and survival terms for older adult bears, which may have reduced survivability in relation to younger adults. After Adult bears reach the 16th age class, they return to that age class indefinitely until death.

3.2 Overview of Parameters

The same comments and limitations mentioned in the Overview of Parameters for the Basic Models, Section 2.2, still apply in this case. Additionally, we are still using the concept of territory (Section 2.4.1) and the existence of 10,000 territories for bears to inhabit at any given time. There are minor differences in how the parameters are used in the Extended Model in terms of density dependence. For example, the weighted survival used in the Basic Model (Section 2.4.2) retains the same form with the exception that the Cubs are not included in the Total Population used in the weighting function Z . Recall,

$$Z[\text{saturated survival}, Total_t] = \text{saturated survival} * e^{(\ln(\text{saturated survival}) * ((\frac{Total_t}{10,000})^8 - 1))}$$

Represents the weighted survival, where $Total_t$ represents the Total population. In the basic model Cubs were included because there was no easy way to separate them from the rest of the bears in the Subadults. Here, it doesn't make sense to keep

the Cubs in the Total population because they share land with their mothers - the breeding females are assumed to have land and resources available in order to have Cubs. Thus, because the breeding females are subject to a weighted survival, this indirectly affects the number of Cubs that can be born each year.

Two new density dependent effects are examined in the following sections: weighted birthrates and weighted harvest rates.

3.2.1 Weighted Birthrates

The method of using a quadratic term with the breeding males and breeding females serves its purpose for population sizes around which the term is balanced. For example, before the term $b_a * A_{f,t} * A_{m,t} * \beta$ was scaled to assume that at 1,000 Adult males and Adult females, the entire term should be approximately equal to $b_a * A_{f,t}$. Thus, while $A_{f,t}, A_{m,t} \approx 1,000$, the birth term scaled properly. As the two populations diverged from 1,000 in either direction, the term grew or shrank rapidly. The new weighted birthrate takes into account the proportion of breeding males to breeding females. A value of 2.35 Cubs per Adult female and 1.1 Cubs per Third Year female (both of the Territorial population, as mentioned in Section 2.2) are incorporated into a function designed to scale the birthrates depending on the number of males available to mate. Consider 2.35 and 1.1 to be the saturated birthrates for Adult females and Third Year females, respectively.

The weighted birthrate is a function of the proportion of breeding males to breeding females, b_r .

Consider the following equation which gives the weighted birthrate for Adult breeding females:

$$\text{Weighted birthrate} = b_a * \left(\frac{\alpha * br^3}{\beta * br^3 + 1} \right).$$

Where br is the breeding ratio - the ratio of breeding males to breeding females, and b_a is the saturated birthrate for Adult female bears. As a reminder, breeding males consist of all Adult males and Third Year males. Breeding females are Third Years and Adult Females up through the 15th Adult Female category which corresponds to age 19 and above.

Both α and β are unitless terms which ensure that the function behaves in a certain manner. The desired behavior would be to have the birthrate be driven towards zero as the proportion of males to females goes towards zero. As the proportion of males

to females reaches a predefined saturation point - that is, the number of breeding males to breeding females is at its most ideal value - we would want the weighted birthrate to equal the saturated birthrate. The nature of the equation used to scale the birthrate also allows for a slight growth in birth as the proportion of breeding males to breeding females tends towards infinity. The last case mentioned (where br tends towards infinity, causing the function to gradually approach a value of approximately $1.27 * b_a$ or $1.27 * b_t$ for Adult females or Third Year females respectively) may not make sense initially. Let us consider what it means for the proportion to tend towards infinity. This would mean that the breeding males greatly outnumber the breeding females, which could occur if you have only one breeding female and, for example, 10,000 breeding males.

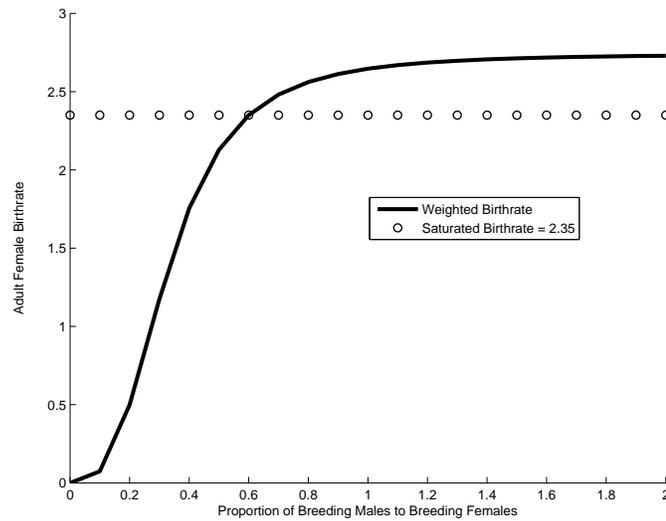


Figure 3.3: Adult female Weighted Birth

In order to facilitate the modeling process, we have assumed that it is always possible for two breeding bears to find each other. Given that, it is realistic to assume that one male bear out of 10,000 will be able to impregnate one breeding female in the population. Most likely, if there is only one breeding female in the population, the population is tending towards extinction in which this nuance has little effect.

Refer to the weighted birth function as $B(br)$. Let us assume that the saturation point is $br = max$. That is, $B(max) = b_a$. Let us also assume that $B(\frac{max}{2}) = \frac{b_a}{2}$. Then we have,

$$b_a * \left(\frac{\alpha * max^3}{\beta * max^3 + 1} \right) = b_a$$

Which implies

$$\left(\frac{\alpha * max^3}{\beta * max^3 + 1} \right) = 1$$

Similarly,

$$b_a * \left(\frac{\alpha * \frac{max^3}{2}}{\beta * 0.3^3 + 1} \right) = \frac{b_a}{2}$$

Which implies

$$\left(\frac{\alpha * \frac{max^3}{2}}{\beta * \frac{max^3}{2} + 1} \right) = \frac{1}{2}$$

It can be shown that $\alpha = \frac{7}{max^3}$ and $\beta = \frac{6}{max^3}$.

For the purposes of the extended model, $max = 0.6$, which yields $\alpha = 32.407$ and $\beta = 27.777$. A graphical representation of weighted birth using these α and β follows in Fig 3.3.

It should be noted that the same function weights the birthrates of both Third Year breeding females, and breeding Adult females - the only difference lies in the replacement of b_a with b_t where the latter is defined as the birthrate for Third Year breeding females.

3.2.2 Weighted Harvest

The logic behind having a weighted harvest has to do with the amount of effort exerted by hunters to kill one bear. One would expect that, as the population tends towards 0, a hunter would need to exert more effort in order to successfully harvest. Let x be the size of a population and y be a harvest rate from Dr. Klenzendorf's thesis. Then, $f(x, y)$ is defined as the weighted harvest. The desired properties for the function are as follows:

$$\text{As } x \rightarrow \infty, f(x) \rightarrow 1$$

$$\text{As } x \rightarrow 0, f(x) \rightarrow 0$$

As $x \rightarrow$ the saturation point, $f(x) \rightarrow$ saturated harvest rate.

Weighted harvest depends on the Total population. The saturation point for all harvest functions is 10,000. The actual function used in the model is

$$X[h_{xy}, Total_t] = \frac{Total_t}{k_{xy} + Total_t}$$

Where $Total$ is the total population at time t , h_{xy} is the saturated harvest of age class x and gender y . and k_{xy} is the saturation constant for a specific age x and gender class y . k_{xy} is found by plugging in the saturation point, 10,000, in for $Total_t$ and setting it equal to the saturated harvest rate for the specific age/gender of bear. The saturated harvest rate is defined as the rate at which bears are harvested when the bear population is saturated (when there are 10,000 bears total), and is the value found in [2] - h_{xy} in Appendix A.5.

$$X[10,000] = \text{saturated harvest}$$

$$\text{saturated harvest} = \frac{10,000}{k_{xy} + 10,000}$$

$$k_{xy} = \frac{10,000 - \text{saturated harvest} * 10,000}{\text{saturated harvest}}.$$

A graphical representation of the function follows in Figure 3.4 for various saturated harvest rates. This does not correspond to any specific age/gender class.

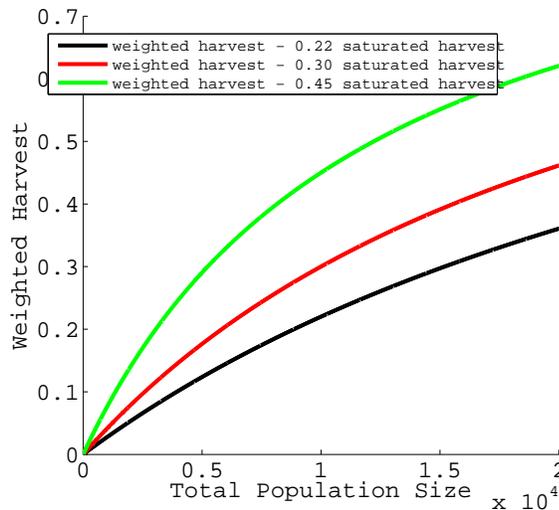


Figure 3.4: Weighted Harvest

When there is a Total Population of 10,000 bears - when the population is saturated - the weighted harvest for Second Year females is equal to the saturated harvest (the value presented in Dr. Klensendorf's thesis). Should the population go above the saturation point of 10,000 bears, the harvest rate increases. As the population grows it is reasonable to expect that the effort a hunter must expend to encounter a suitable bear decreases. Though the graph does not explicitly show the long term behavior for the function, it is easy to see from the function itself that as the population approaches infinity, the weighted harvest approaches 100%. The higher the saturated

harvest rate, the quicker that the weighted harvest approaches 1 after passing a Total population size of 10,000 bear. This might not be entirely realistic; should a population reach incredibly large sizes, it might be the case that hunters are unable to keep up with the growth of the bear population, and the weighted harvest would decrease. However, the approach used in the Extended Model should be valid for cases near the initial conditions used for the model. As long as the population remains within a certain ϵ of the initial population, we can expect dynamics shown in Figure 3.4. This type of approach promotes a natural equilibrium based on the varying amounts of effort that must be exerted by hunters with a constantly varying population size.

All weighted harvest functions for all age and gender combinations share the same form of the previous example, save for varying saturated harvest rates based on age and gender.

3.3 Assumptions

Many assumptions were listed through the course of Chapter 3. Here there are a few more comments and clarifications on the major assumptions of the Extended Model. Note that most assumptions were dealt with in Section 2.3.1 and throughout the paper. Any deviations from the set of assumptions on the Basic Models are mentioned here.

In terms of birth, it is assumed that no female bear over the age of 20 reproduces. It has been observed that a female bear can reproduce until age 25. As currently modeled, the adult females exit the breeding pools after age 19. This may be unrealistic, but reflects data found in source [2].

Having each weighted harvest function dependent upon the Total population assumes that an increase in one sub-population such as Third Year males will cause an increase in harvest for all of the sub-populations. The alternative was to have each weighted harvest function only dependent upon the age/gender class that it is associated with. However, in order to do this there would have to be some assumed saturation point for each and every age and gender class mentioned in the Extended Model. Overall this would impose too many arbitrary restrictions on the populations, because no data in the literature discusses individual age/gender carrying capacities. Additionally, as mentioned, using individual saturation points for the age/gender categories would be too rigid of an assumption that would restrict the ability of one age/gender class to expand based on open territories. If a territory were open yet a given age/gender class was above its saturation point, it would be unable to grow

and fill out the population. The weighted harvest does not take into account differing encounter rates between hunters and specific individual age/gender classes - the assumption is that the distribution of all age/gender classes in space is roughly homogeneous.

Finally, in the Matlab code used to simulate this population, it is assumed that, should any population have less than 1 bear in it, it will be counted as zero bears. This applies to all age/gender/territory classes. Similarly there are restrictions placed in the matlab code so that the weighted harvest will never exceed the weighted survival at a given time step. Even though the harvest rate and survival rate are being weighted by a function, they must still sum to 1.

3.4 Equations

The equations listed hereafter are only the female equations - the male equations are identical. A quick note - the function $Z[s_{xy}, Total]$ is the weighted harvest of age/gender class x/y , derived in Section 2.4.2. The same behavior occurs in the weighted survival of the Extended Model.

3.4.1 Cubs

The first equation we will examine concerns the Cub population.

$$C_{t+1} = b_t * p_f * \left(\frac{\alpha * br^3}{\beta * br^3 + 1} \right) * T_{f,t} + b_a * p_f * \left(\frac{\alpha * br^3}{\beta * br^3 + 1} \right) * FA_t.$$

Where C_{t+1} are the Cubs in year $t+1$, br is the ratio of breeding males to breeding females at time t , FA_t are the breeding females at time t , b_t is the birthrate for third year females, p_f is the percentage of females which breed in any given year, and b_a is the adult female birthrate. Both α and β are scaling terms, derived fully in Section 3.2.1.

FA_t , breeding adult females, include all Adult Female Age classes 1 through 15. Adult Female Age class 16 is considered out of the breeding pool. The term $\frac{\alpha * br^3}{\beta * br^3 + 1}$ was mentioned in Section 3.2.1; it acts as weighted birthrates for breeding adult females, and breeding third year females. Then the actual number of breeding females in any given year, given by $p_f * T_{f,t}$ and $p_f * FA_t$, are multiplied by the weighted birthrates to obtain the number of Cubs. Cubs are not classified by gender, as there is, roughly, a 1:1 male to female ratio of Cubs [2]. These are not counted as part of the Total

Population used to weight survival and harvest. As mentioned, this has to do with the assumption that any female which breeds does so with the required amount of resources available to her in order to successfully conceive. As the breeding females are subject to weighted survival and harvest, this indirectly affects the Cubs that are born.

3.4.2 First Year Bears

The next age class, following the Cubs, are the first year bears.

$$F_{f,t+1} = 0.5 * (s_c - h_c) * C_t.$$

Where $F_{f,t+1}$ are the First Year females, s_c is the saturated cub survival, and h_c is the saturated cub harvest. As a reminder, C_t is the Cub population.

Because there is a 1:1 male to female ratio in the Cub population, it follows that $0.5 * C_t$ would give the number of female Cubs. Then, $s_c - h_c$, cub survival rate less cub harvest rate, would yield the percentage of Cubs still alive after one year. The result would be the number of Roaming First Year female Cubs. Recall the assumption that density dependent effects do not affect Cubs; Cubs are indirectly affected by the weighted harvest and survival based on the availability of breeding females.

3.4.3 Second Year Bears

Second Year bears are the first age class to use the weighted harvest and survival functions mentioned in Sections 3.2.2, 2.4.2. The Second Year Female equation is as follows:

$$S_{f,t+1} = (Z[s_{ff}, Total_t] - X[h_{ff}, Total_t]) * F_{f,t}.$$

Where s_{ff} is the saturated survival of First Year females, and h_{ff} is the saturated harvest for both First Year females. $F_{f,t}$ is, again the equation for the First Year females.

3.4.4 Third Year Bears

The Third Year bear equation is identical in behavior to the Second Year bear equation.

$$T_{f,t+1} = (Z[s_{sf}, Total_t] - X[h_{sf}, Total_t]) * S_{f,t}.$$

Where $T_{f,t+1}$ are the Third Year females, s_{sf} is the saturated survival for Second Year females, and h_{sf} is the saturated harvest for the second year females.

3.4.5 Adults

The final age class discussed in Section 3.4 are the Adult females. These equations are, again, identical with regard to behavior to the Third Year females and the Second Year females. However, there are three separate types of equations with minor changes to account for small differences between the various stages of adulthood. These reflect the 16 distinct stages of adulthood in this model.

The first stage of adulthood is obtained with the following equation:

$$A_{f,t+1} = (Z[s_{tf}, Total_t] - X[h_{tf}, Total_t]) * T_{f,t}.$$

Where $A_{f,t+1}$ are the Adult females, stage one. s_{tf} is the saturated survival rate for Third Year females; h_{tf} is the saturated harvest rate for Third Year females, and $T_{f,t}$ are the Third Year Landed females.

Then, the following equation governs the behavior from Adult female stage 2 until until Adult female stage 13.

$$A_{fn,t+1} = (Z[s_{af}, Total_t] - X[h_{af}, Total_t]) * A_{f(n-1),t}.$$

$$n \in \{2, \dots, 13\}$$

Where $A_{fn,t+1}$ is the Adult female class, stage n . s_{af} is the saturated adult female survival rate, and h_{af} is the saturated adult female harvest rate. The difference between these equations and the stage 1 equation has to do with the dependence of stage 1 Adult females on the Third Year female population. After that, stage 2 through stage 13 Adult females depend upon previous stages of Adult females. We have assumed that stage 2 through stage 13 females have the same saturated survival and saturated harvest rates. That is why s_{af} and h_{af} are used in each of the 11 equations. Stages 14, 15, and 16, however, use different survival rates to account for old age.

$$A_{f14,t+1} = (Z[s_{af13}, Total_t] - X[h_{af}, Total_t]) * A_{f13,t}$$

$$A_{f15,t+1} = (Z[s_{af14}, Total_t] - X[h_{af}, Total_t]) * A_{f14,t}$$

$$A_{f16,t+1} = (Z[s_{af15}, Total_t] - X[h_{af}, Total_t]) * A_{f15,t} \\ + 0.05 * (Z[s_{af16}, Total_t] - X[h_{af}, Total_t]) * A_{f16,t}$$

In order to account for an additional age factor in the survivability of Adult Landed female stages 14 through 15, updated and distinct survival rates are used for these three equations: $s_{af13} = \frac{1}{2} * s_f$, $s_{af14} = \frac{1}{2} * s_{af13}$, $s_{af15} = \frac{1}{2} * s_{af14}$, $s_{af16} = \frac{1}{2} * s_{af15}$. This may not be entirely true biologically, but it fixes problems the model encountered in test cases where the Total population reached extremely low numbers. When that occurred, age class 16 bears would survive for an unrealistically long amount of time because the weighted survival was close to 100%. The 0.05 in front of the second part of the $A_{f16,t+1}$ term is an additional old age term. Though the survival terms for $A_{f13}, A_{f14}, A_{f15}, A_{f16}$ are halved at each step up in age class, the weighted survival can still tend towards 100% as the population declines. Thus, the 0.05 ensures that the bears will live approximately 5 years upon their entering the A_{f16} age class.

3.5 Results and Discussion

All simulations were run with a starting population of 8,000 bears distributed arbitrarily amongst the age and gender classes. The number of territories available are 10,000 (as mentioned). All other relevant parameters such as saturated harvest/survival rates, and saturation constants (etc.) can be found in Appendix A.5.

The first simulation is run with saturated harvest rates (again, found in Appendix A.5) obtained directly from Dr. Klenzendorf's thesis. Recall that the saturated harvest rates are defined as the harvest rate of a saturated population - 10,000 bears. Saturated survival and birthrates use similar logic. This preliminary simulation gives an depiction of the black bear population with 2002 harvest rates.

In Figure 3.5, the proportions of males to females over time do not include the cub population - as it would be a 1:1 split and would not affect the proportions. There is an eventual stabilized gender proportion at approximately 60% female to

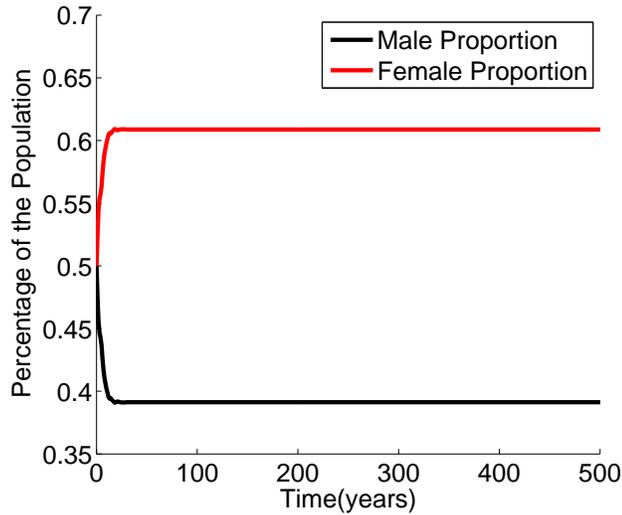


Figure 3.5: Population Proportions, Harvest in Appendix A.5, Initial total 8,000 bears

40% male. This seems like a reasonable estimate given the observed proportion at Dr. Klenzendorf’s study site - 0.6Males:1Female.

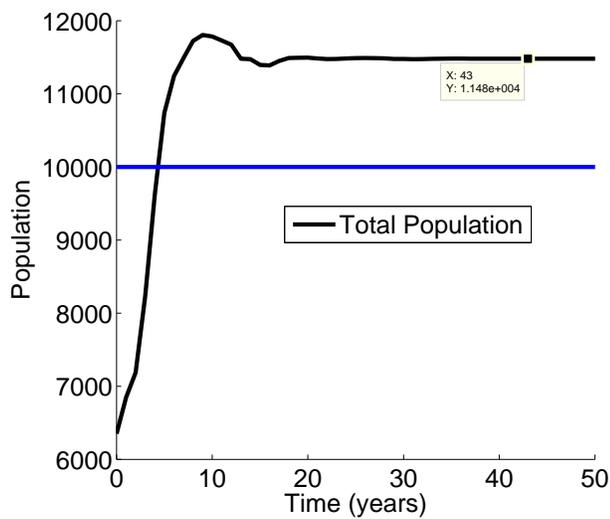


Figure 3.6: Total Population, Harvest in Appendix A.5, Initial total 8,000 bears

Figure 3.6 shows the Total black bear population without Cubs, and Figure 3.7. Notice that the population increases to approximately 11,800, and then declines and stabilizes to an approximate population of 11,480 bears. When one considers that there are 4181 Cubs at equilibrium, we get a total population estimate of 15,881 which is very close to the estimate given by the second version of the Basic Model (Section 2.4.4, Figure 2.16) which yielded 16,980 bears include all age and gender categories under the effects of a constant harvest of 100 bears in Subadult males and females,

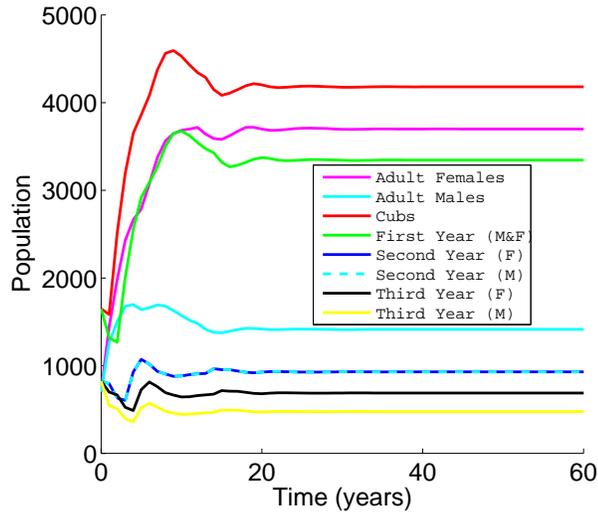


Figure 3.7: Population Break Down, Harvest in Appendix A.5, Initial total 8,000 bears

and Adult males and females. The steady state solution shown in Figure 3.6 is not sensitive to initial conditions.

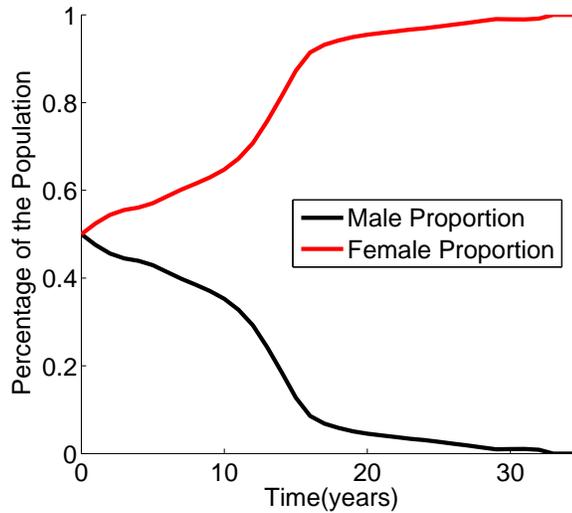


Figure 3.8: Proportions, 12 years of saturated harvest growth, Initial total 8000 bears

A natural question to ask is how much of an increase in saturated harvest causes the black bear population to go towards extinction. Subsequent simulations were run under identical initial conditions, with the exception of an increased saturated harvest rate. After each iteration, the saturated harvest was increased by 7.4% (per the information found by the VDGIF [6]). Increasing the saturated harvest rate changes the weighted harvest.

The simulations reveal that it takes 12 years of saturated harvest increase at

7.4% per year to cause the population to go towards extinction. Though that would mean that, for example, the saturated harvest of the Second Year Males would be approximately 99% (all harvest rates are capped at 99% to ensure the code's stability) we must also keep in mind that a 99% saturated harvest is not necessarily the weighted harvest. Figure 3.9 shows the change in the weighted harvest of the Second Year males. Around year 12 the weighted harvest of the Second Year males is close to 100%. As seen in Figure 3.10 between the twelfth and thirteenth iteration, this results in only 15.33 of the 809.1 Second Year males to enter the Third Year male population - that is a harvest of approximately 796 bears which may be a bit unrealistic but is, perhaps, feasible.

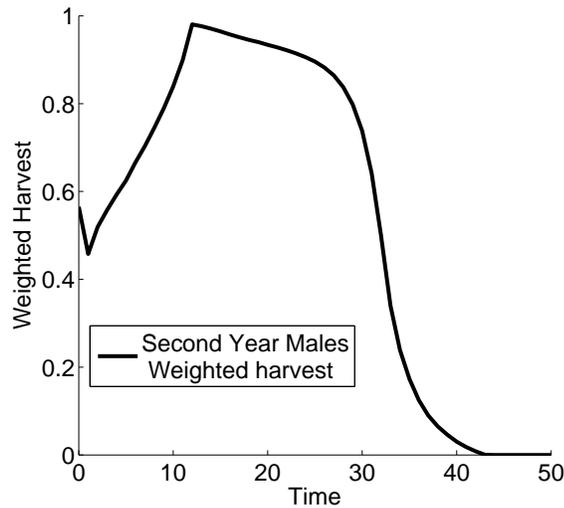


Figure 3.9: Second Year Male Weighted Harvest (12 Years Growth)

Figure 3.8 shows that the male proportion reaches 0 in year 33 - corresponding to year 2035. This figure also suggests that it is the decline of the male population that eventually drives the population towards extinction - not the female population. Suppose that the Second Year male saturated harvest is not allowed to grow by 7.4% per year, and remains at 45%. The simulations show that saturated harvest must grow for 18 years in order to cause the population to tend towards extinction. More so than the Basic Models, the Extended Model shows that it is the harvest of the Second Year male population which leads to the extinction of the population, based on the present information. Of course, this method of increasing the saturated harvest is not perfect - in year 12 it was shown that the weighted harvest of Second Year males was $\approx 98\%$ of the Second Year male population.

It is precisely for this reason that the male bears were included in this model in the first place - a model showing only females might show that the population is nonzero

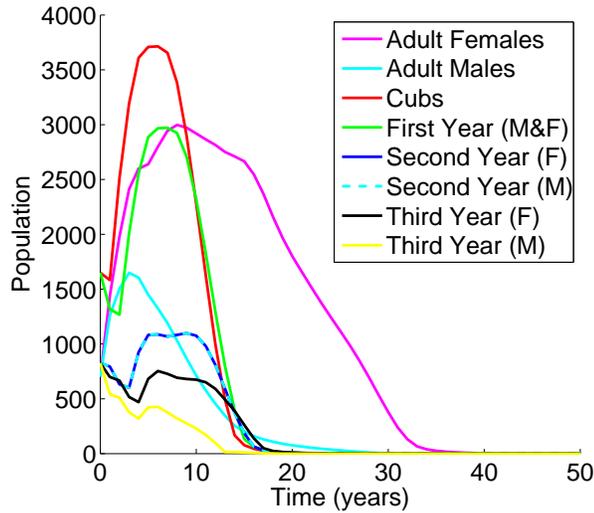


Figure 3.10: Population Breakdown, 12 years of saturated harvest growth, Initial total 8000 bears

and stable after 12 years of increased harvest.

It also serves as an interesting study to examine the behavior of the system after 11 years of saturated harvest increase.

Figure 3.11, 3.12, and 3.13 all suggest that something causes the population to be driven downwards before it recovers. Let us examine the value of the weighted harvest with 11 years of growth in saturated harvest - it can be seen in Figure 3.14. As the population size starts to approach its equilibrium value of approximately 12,000 bears, the weighted harvest of the Second Year males is increased drastically, which most likely forces the population down again, towards extinction.

Another series of simulations were run with a starting population of 20,000 bears. For 0 years of increase in harvest, the populations limit on to the same steady state solution as the simulation with only 8,000 bears (refer to Figure 3.6). When a simulation is run with a starting population of 20,000 and 12 years of growth in saturated harvest, the Black Bear population still tends towards extinction. At 11 years of growth in saturated harvest, the population persists. In another simulation with an initial population of 80,000 bears, the population still tends towards extinction after 12 years of growth in saturated harvest.

This suggests that there may exist a basin of attraction between (8000, 20000) for the case when there is no growth in the saturated harvest rate - it is very likely that the equilibrium solution shown in the simulations is globally stable. There may exist cases between (8000, 20000) which do not limit towards the Total Population (without Cubs) of 11,820 bears, the apparent steady state solution for original satu-

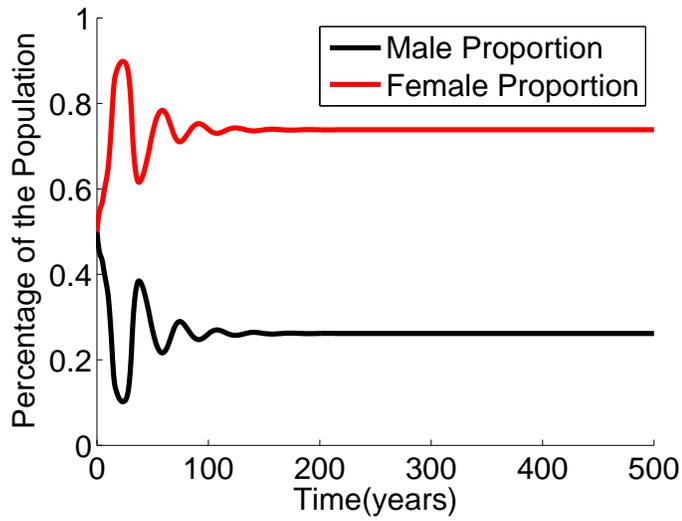


Figure 3.11: Proportions, 11 years of saturated harvest growth, Initial total 8000 bears

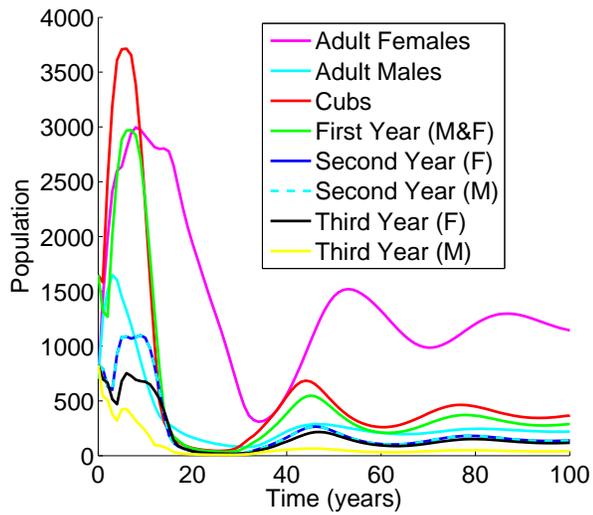


Figure 3.12: Population Breakdown, 11 years of saturated harvest growth, Initial total 8000 bears

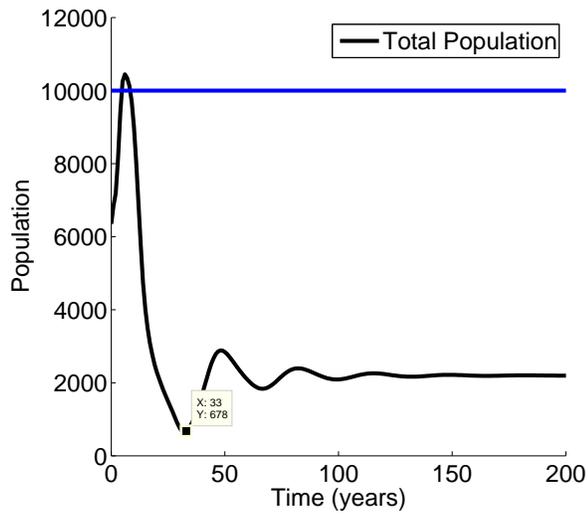


Figure 3.13: Total Population, 11 years of saturated harvest growth, Initial total 8000 bears

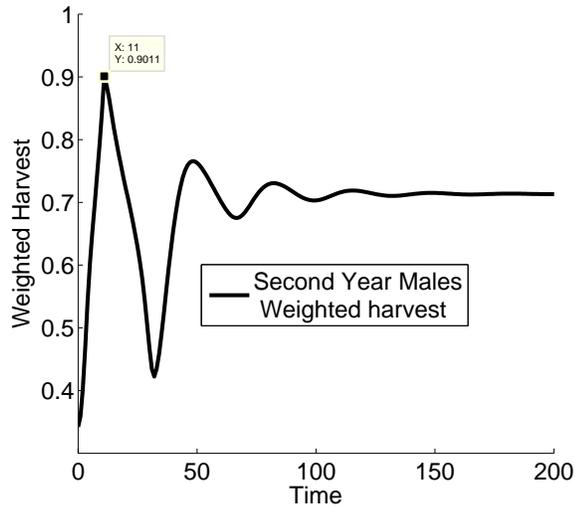


Figure 3.14: Second Year Weighted Harvest - 11 Years Harvest Growth

rated harvest rates (Appendix A.5. Changing the saturated harvest rate causes the equilibrium solution to be at lower population values with respect to equilibria with lower saturated harvest rates; this does not come as a surprise given that the saturated harvest rate affects the weighted harvest - a term dependent upon the carrying capacity implemented in this population model.

3.6 Ending Remarks

There are many mechanisms in this model to ensure the survival of the black bear population - the weighted harvest and survival rates are designed to add flexibility to the parameters, which would not exist with strictly linear terms. Additionally, as shown in the previous results, the importance of considering the Male black bears as a distinct entity within the model is without question. The high harvesting of male bears shown in the simulations eventually puts a strain on the black bear population from which they cannot recover. However, these mechanisms may also provide an unrealistic persistence to the black bear population. If we were to give credence to the simulations run, there are only 6 more years of harvest growth before we reach the point at which the model predicts the decline and eventual extinction of the bear population given the methods used to model the black bear population. This is because we have assumed that 0 years of harvest growth corresponds to year 2002 and thus 13 years of harvest growth corresponds to year 2015.

The weighted harvest, in particular, is the most suspect term in the model.

Chapter 4

Conclusion

The two versions of the Basic Model, in addition to the Extended Model, offer a wealth of information concerning the dynamics of the Black Bear population under the effects of harvesting. The insight to be gained from the analysis and simulations can be used to make informed decisions concerning the management of the Black Bear population. Some of the items listed as options in the management plan published by the VDGIF [4] included “allowing nature to take its course”, “influencing nonhunting mortality”, and “fertility control” as viable methods to control the Black Bear population. Furthermore, they cite growth in the Black Bear population as an indication that the Black Bear population requires management. Many of the simulations reveal that, even though the population may be experiencing growth, it may still be on the way to becoming extinct. With that said, utilizing the simulations to predict the extinction of the Black Bear population must be done so extremely conservatively because the dynamics of the Black Bear population are complex.

Future work entails interviewing a worker at the Virginia Department of Game and Inland Fisheries, stationed in Richmond, Virginia, in order to better explain the project and gain some insight on ways to increase the validity of the models. Additionally, there are many assumptions which could easily be relaxed upon further research into the behavioral characteristics of the bear population. On a broader scope, linking Virginia’s Black Bear Population with other black bear populations along the Southern Appalachians - in North and South Carolina, Alabama, and Georgia, would be an interesting study of more global black bear trends. The Black Bear population could be split into a Roaming and Territorial population to allow for the transfer of bears between areas. Furthermore, additional mathematical analysis on the models described in this paper can be done through the use of computational homology. There are two programs - GAIO [1] and CHoMP [3] which can be used to better understand the characteristics of a dynamical system.

GAIO utilizes interval arithmetic to compute outer approximation of the map of

a given system; it divides all possible initial population conditions into increasingly smaller boxes. By refining these intervals, the resolution of the map becomes clearer (though the computational cost rises at higher resolutions). The Basic Versions of the model, in particular, would be useful to examine in conjunction with GAIO and CHoMP. The algorithms, based on topological and homological theory, these programs allow for computer assisted proofs concerning steady state solutions, periodic solutions, and more complicated dynamics such as basins of attraction and chaos. Additionally, the algorithms can be used with different parameter values in order to examine the topology and homology of a dynamical system - this would be extremely useful to examine, as most of the parameters used in the model are known within a certain confidence interval.

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Appendix A

A.1 Electronic Appendix

A collection of Matlab files used to run the simulations found in this thesis will be available at the following URL:

<http://math.wm.edu/~sday/students.html>

A.2 Parameters as Functions

A.2.1 Weighted Survival

s_{xy} —The survival rate of age class x , and gender y . Recall that cubs, First Year Bears, and Second Year Bears are considered Subadults.

$x \in \{\text{Cubs}(c), \text{First Year Bears}(f), \text{Second Year Bears}(s),$

$\text{Third Year Bears}(t), \text{Adults}(a)\},$

$y \in \{\text{males}(m), \text{females}(f)\}.$

$Total_t$ —The total population at time t including all age and gender classes.

Let Z be a function of survival of age class x and gender y as defined above.

$$Z[s_{xy}, Total_t] = s_{xy} * e^{\left(\ln(s_{xy}) * \left(\left(\frac{Total_t}{10000}\right)^8 - 1\right)\right)}$$

A.2.2 Weighted Harvest

h_{xy} —The harvest rate of age class x , and gender y . Recall that cubs, First Year Bears, and Second Year Bears are considered Subadults.

$x \in \{\text{Cubs}(c), \text{First Year Bears}(f), \text{Second Year Bears}(s),$

$\text{Third Year Bears}(t), \text{Adults}(a)\},$

$y \in \{\text{males}(m), \text{females}(f)\}.$

k_{xy} —The saturation constant, derived below, for age class x and gender y where x and y are defined as above

$Total_t$ —The total population at time t including all Subadult males/females, and Adult males/females

$$X[h_{xy}, Total_t] = \frac{Total_t}{k_{xy} + Total_t}$$

k_{xy} is found by plugging in the saturation point, 10,000, in for $Total_t$ and setting it equal to the saturated harvest rate for the specific age/gender of bear. The saturated harvest rate is defined as the rate at which bears are harvested when the bear population is saturated (when there are 10,000 bears total).

$$X[10,000] = \frac{10,000}{k_{xy} + 10,000} = h_{xy}$$

$$h_{xy} = \frac{10,000}{k_{xy} + 10,000}$$

$$k_{xy} = \frac{10,000 - h_{xy} * 10,000}{h_{xy}}.$$

There is a distinct k_{xy} for all harvest rates, h_{xy} .

A.2.3 Weighted Birthrate

*The Weighted Birthrate is only used in the Extended Model.

b_x —The birthrate of females in age class x where $x \in$

{Adult Females (a), Third Year Females (t)}

br —The ratio of breeding males to breeding females. Breeding males include all Third Year males in addition to all Adult males, $A_{mn,t}$, for all $n \in \{1, \dots, 16\}$ - stage 1 through 16, as defined in the Extended model. Breeding females include all Third Year females and all Adult females, $A_{fn,t}$, for $n \in 1, \dots, 15$.

Note the exclusion of $A_{f16,t}$.

α, β —Constants used to scale the Weighted Birth term.

$$\text{Weighted birthrate} = b_x * \left(\frac{\alpha * br^3}{\beta * br^3 + 1} \right)$$

Refer to the weighted birth function as $B(br)$. Let us assume that the saturation point is $br = max$. That is, $B(max) = b_a$. Let us also assume that $B(\frac{max}{2}) = \frac{b_a}{2}$. Then we have,

$$b_a * \left(\frac{\alpha * max^3}{\beta * max^3 + 1} \right) = b_a$$

Which implies

$$\left(\frac{\alpha * max^3}{\beta * max^3 + 1} \right) = 1$$

Similarly,

$$b_a * \left(\frac{\alpha * \frac{max^3}{2}}{\beta * 0.3^3 + 1} \right) = \frac{b_a}{2}$$

Which implies

$$\left(\frac{\alpha * \frac{max^3}{2}}{\beta * \frac{max^3}{2} + 1} \right) = \frac{1}{2}$$

It can be shown that $\alpha = \frac{7}{max^3}$ and $\beta = \frac{6}{max^3}$.

For the purposes of the extended model, $max = 0.6$, which yields $\alpha = 32.407$ and $\beta = 27.777$.

A.3 Basic Model

A.3.1 Equations - Basic Model Version 1

$S_{f,t}$ – Subadult female Bears at time t.

p_f – The proportion of females that breed in any given year.

b_t – The birthrate of Third Year females.

β_1 – A term which weights the number of cubs for Third Year females.

β_2 – A term which weights the number of cubs for Adult females.

$A_{m,t}$ – Adult male Bears at time t. This category includes any male bear which is three years of age, or older.

$A_{f,t}$ – Adult female Bears at time t. This category includes any female bear which is three years of age, or older.

v_{xy} – The proportion of age class x , and gender y . Recall that cubs, First Year Bears, and Second Year Bears are considered Subadults.

$x \in \{\text{Cubs } (c), \text{First Year Bears } (f), \text{Second Year Bears } (s), \text{Third Year Bears } (t), \text{Adults } (a)\},$

$y \in \{\text{males } (m), \text{females } (f)\}.$

b_a – The birthrate of female bears above the age of three.

s_{xy} – The survival rate of age class x and gender y , where x and y are defined as above.

h_{xy} – The harvest rate of age class x and gender y , where x and y are defined as above.

Subadult Males

$$S_{m,t+1} = 0.5 * p_f * b_t * \beta_1 * v_{tf} * A_{f,t} * A_{m,t} + 0.5 * p_f * b_a * \beta_2 * v_{af} * A_{f,t} * A_{m,t} \\ + (s_{cm} - h_{cm}) * v_{cm} * S_{m,t} + (s_{fm} - h_{fm}) * v_{fm} * S_{m,t}$$

Subadult females

$$S_{f,t+1} = 0.5 * p_f * b_t * \beta_1 * v_{tf} * A_{f,t} * A_{m,t} + 0.5 * p_f * b_a * \beta_2 * v_{af} * A_{f,t} * A_{m,t} \\ + (s_{cf} - h_{cf}) * v_{cf} * S_{f,t} + (s_{ff} - h_{ff}) * v_{ff} * S_{f,t}$$

Adult males

$$A_{m,t+1} = (s_{sm} - h_{sm}) * v_{sm} * S_{m,t} + (s_{tm} - h_{tm}) * v_{tm} * A_{m,t} \\ + (s_{am} - h_{am}) * v_{am} * A_{m,t}$$

Adult females

$$A_{f,t+1} = (s_{sf} - h_{sf}) * v_{sf} * S_{f,t} + (s_{tf} - h_{tf}) * v_{tf} * A_{f,t} \\ + (s_{af} - h_{af}) * v_{af} * A_{f,t}$$

A.3.2 Equations - Basic Model Version 2

$S_{f,t}$ —Subadult female Bears at time t .

p_f —The proportion of females that breed in any given year.

b_t —The birthrate of Third Year females.

$A_{m,t}$ —Adult male Bears at time t . This category includes any male bear which is three years of age, or older.

$A_{f,t}$ —Adult female Bears at time t . This category includes any female bear which is three years of age, or older.

v_{xy} —The proportion of age class x , and gender y . Recall that cubs, First Year Bears, and Second Year Bears are considered Subadults.

$x \in \{\text{Cubs}(c), \text{First Year Bears}(f), \text{Second Year Bears}(s),$

$\text{Third Year Bears}(t), \text{Adults}(a)\}$,

$y \in \{\text{males}(m), \text{females}(f)\}$.

b_a —The birthrate of female bears above the age of three.

s_{xy} —The saturated survival rate of age class x and gender y , where x and y are defined as above.

h_i —The constant harvest of age class $i \in$

$\{\text{Subadult males (1), Subadult females (2), Adult males (3),$

$\text{Adult females}(4)\}$

$Z[s_{xy}, Total_t]$ —The weighted survival function, with x, y defined as above.

This is derived in Section 2.4.2.

Subadult males

$$S_{m,t+1} = \max\{0, 0.5 * p_f * b_t * v_{tf} * A_{f,t} * A_{m,t} * \beta + 0.5 * p_f * b_a * A_{f,t} * A_{m,t} * \beta + (s_{cm}) * v_{cm} * S_{m,t} + (Z[s_{fm}, Total_t]) * v_{fm} * S_{m,t} - h_1\}$$

*Recall that the Cubs are not subject to a weighted survival rate: Section 2.4.2.

Subadult females

$$S_{f,t+1} = \max\{0, 0.5 * p_f * b_t * v_{tf} * A_{f,t} * A_{m,t} * \beta + 0.5 * p_f * b_a * A_{f,t} * A_{m,t} * \beta + (s_{cf}) * v_{cf} * S_{f,t} + (Z[s_{ff}, Total_t]) * v_{ff} * S_{f,t} - h_2\}$$

Adult males

$$A_{m,t+1} = \max\{0, (Z[s_{sm}, Total_t]) * v_{sm} * S_{m,t} + (Z[s_{tm}, Total_t]) * v_{am} * A_{m,t} + (Z[s_{am}, Total_t]) * A_{m,t} - h_3\}$$

Adult females

$$A_{f,t+1} = \max\{0, (Z[s_{sf}, Total_t]) * v_{sf} * S_{f,t} + (Z[s_{tf}, Total_t]) * v_{af} * A_{f,t} + (Z[s_{af}, Total_t]) * A_{f,t} - h_4\}$$

A.4 Equations - the Extended Model

C_t – male and female cubs at time t.

$F_{m,t}$ – First Year males at time t.

$F_{f,t}$ – First Year females at time t.

$S_{m,t}$ – Second Year males at time t.

$S_{f,t}$ – Second Year females at time t.

$T_{m,t}$ – Third year males at time t; they have the ability to reproduce.

$T_{f,t}$ – Third year females at time t; they have the ability to reproduce.

$A_{mn,t}$ – Adult males at time t in age class n, $n \in \{1, 2, \dots, 16\}$.

$A_{fn,t}$ – Adult females at time t in age class n, $n \in \{1, 2, \dots, 16\}$.

$Total_t$ – total population at time t; includes

$F_m, F_f, S_m, S_f, T_m, T_f, A_{mn}, A_{fn}$. Note

the exclusion of the Cubs in the Total population.

$Total_t$ – the total population - includes all gender, age, and territory classes.

b_x – The birthrate of females in age class x where $x \in$

$\{\text{Adult Females } (a), \text{Third Year Females } (t)\}$

br – The ratio of breeding males to breeding females. Breeding males include

all Third Year males in addition to all Adult males, $A_{mn,t}$, for all

$n \in \{1, \dots, 16\}$ - stage 1 through 16, as defined in the Extended model.

Breeding females include all Third Year females and all Adult females, $A_{fn,t}$,

for $n \in 1, \dots, 15$. Note the exclusion of $A_{f16,t}$.

α, β – Constants used to scale the Weighted Birth term.

$$C_{t+1} = b_t * p_f * \left(\frac{\alpha * br^3}{\beta * br^3 + 1} \right) * T_{f,t} + b_a * p_f * \left(\frac{\alpha * br^3}{\beta * br^3 + 1} \right) * FA_t$$

$$F_{m,t+1} = 0.5 * (s_c - h_c) * C_t$$

$$F_{f,t+1} = 0.5 * (s_c - h_c) * C_t$$

$$S_{m,t+1} = (Z[s_{fm}, Total_t] - X[h_{fm}, Total_t]) * F_{m,t}$$

$$S_{f,t+1} = (Z[s_{ff}, Total_t] - X[h_{ff}, Total_t]) * F_{f,t}$$

$$T_{m,t+1} = (Z[s_{sm}, Total_t] - X[h_{sm}, Total_t]) * S_{m,t}$$

$$T_{f,t+1} = (Z[s_{sf}, Total_t] - X[h_{sf}, Total_t]) * S_{f,t}$$

$$A_{m,t+1} = (Z[s_{tm}, Total_t] - X[h_{tm}, Total_t]) * T_{m,t}$$

$$A_{mn,t+1} = (Z[s_{am}, Total_t] - X[h_{am}, Total_t]) * A_{m(n-1),t}$$

$$n \in \{2, \dots, 13\}$$

$$A_{mn,t+1} = (Z[s_{am(n-1)}, Total_t] - X[h_{am(n-1)}, Total_t]) * A_{m(n-1),t}$$

$$n \in \{14, 15, 16\}$$

$$A_{f,t+1} = (Z[s_{tf}, Total_t] - X[h_{tf}, Total_t]) * T_{f,t}$$

$$A_{fn,t+1} = (Z[s_{af}, Total_t] - X[h_{af}, Total_t]) * A_{f(n-1),t}$$

$$n \in \{2, \dots, 13\}$$

$$A_{fn,t+1} = (Z[s_{af(n-1)}, Total_t] - X[h_{af(n-1)}, Total_t]) * A_{f(n-1),t}$$

$$n \in \{14, \dots, 16\}$$

$$A_{f16,t+1} = (Z[s_{a15}, Total_t] - X[h_{af15}, Total_t]) * A_{f15,t}$$

$$+ (Z[s_{a16}, Total_t] - X[h_{af16}, Total_t]) * A_{f16,t}$$

A.5 Parameters

Parameter	Units	Value(s)	Source
b_a - Adult female birthrate	cubs per Adult female	2.35	Klenzendorf, Sybille [2]
b_t - Third year female birthrate	cubs per Third year female	1.1	Klenzendorf, Sybille [2]
p_f - percentage of breeding females	percentage	0.55	Klenzendorf, Sybille [2]
α - birth weighting term	unitless	32.407	calculation
β - birth weighting term	unitless	27.777	calculation
max - the proportion of breeding males to breeding females, b_r , necessary to achieve the saturated birthrate, b_a or b_t	percentage	0.6	estimate
s_c - cub survival	percentage	0.80	VDGIF [5]
s_{ff} - First Year female survival	percentage	0.85	estimate
s_{fm} - First Year male survival	percentage	0.85	estimate
s_{sf} - Second Year female survival	percentage; territory based, roaming	0.995	Klenzendorf, Sybille [2]

Table A.1: Parameters - Birth terms, Survival terms

Parameter	Units	Value(s)	Source
s_{sm} - Second Year male survival	percentage	0.999	Klenzendorf, Sybille [2]
s_{tf} - Third year female survival	percentage	0.995	Klenzendorf, Sybille [2]
s_{tm} - Third year male survival	percentage	0.999	Klenzendorf, Sybille [2]
s_{af} - Adult female survival	percentage	0.998	Klenzendorf, Sybille [2]
s_{afi} where $i \in \{13, \dots, 16\}$ - female survival for $A_f i$	percentage	0.499, 0.2495, 0.12475, 0.062375, respectively	estimate
s_{am} - Adult male survival	percentage	0.999	Klenzendorf, Sybille [2]
s_{ami} where $i \in \{13, \dots, 16\}$ male survival for $A_m i$	percentage	0.4995, 0.24975, 0.124875, 0.0624375, respectively	estimate
h_c - Cub harvesting (not distinguished by gender)	percentage	0	estimate
h_{ff} - First Year female harvest	percentage	0.05	estimate
h_{fm} - First Year male harvest	percentage	0.05	estimate
h_{sf} - Second Year female harvest	percentage	0.22	Klenzendorf, Sybille [2]
h_{sm} - Second Year male harvest	percentage	0.45	Klenzendorf, Sybille [2]

Table A.2: Parameters - Survival cont., Harvest rates

Parameter	Units	Value(s)	Source
h_{tf} - Third year female harvest	percentage	0.05	Klenzendorf, Sybille [2]
h_{tm} - Third year male harvest	percentage	0.30	Klenzendorf, Sybille [2]
h_{af} - Adult female harvest	percentage	0.13	Klenzendorf, Sybille [2]
h_{am} - Adult male harvest	percentage	0.19	Klenzendorf, Sybille [2]
h_1 - Subadult female constant harvest	bears	varies	estimates based on [6]
h_2 - Subadult male constant harvest	bears	varies	estimates based on [6]
h_3 - Adult female constant harvest	bears	varies	estimates based on [6]
h_4 - Adult male constant harvest	bears	varies	estimates based on [6]
v_{cm} - the proportion of Cubs in Subadult males	percentage	0.5185	simulation, Figure 3.7
v_{fm} - the proportion of First Years in Subadult males	percentage	0.4096	simulation, Figure 3.7
v_{sm} - the proportion of Second Years in Subadult males	percentage	0.0719	simulation, Figure 3.7

Table A.3: Parameters - Harvest rates cont., Constant Harvest, Population Proportions

Parameter	Units	Value(s)	Source
v_{cf} - the proportion of Cubs in Subadult females	percentage	0.5186	simulation, Figure 3.7
v_{ff} - the proportion of First Years in Subadult females	percentage	0.4096	simulation, Figure 3.7
v_{sf} - the proportion of Second Years in Subadult females	percentage	0.0719	simulation, Figure 3.7
v_{tm} - the proportion of Third Years in Adult males	percentage	0.083	simulation, Figure 3.7
v_{am} - the proportion of bears over the age of three in Adult males	percentage	0.9170	simulation, Figure 3.7
v_{tf} - the proportion of Third Years in Adult females	percentage	0.0909	simulation, Figure 3.7
v_{af} - the proportion of bears over the age of three in Adult females	percentage	0.9091	simulation, Figure 3.7
k_{of} - saturation constant, First Year females	bears	190,000	$\frac{(10000)*(1-h_{ff})}{h_{ff}}$
k_{om} - saturation constant, First Year males	bears	190,000	$\frac{(10000)*(1-h_{fm})}{h_{fm}}$
k_{sf} - saturation constant, Second Year females	bears	$3.5455 * 10^4$	$\frac{(10000)*(1-h_{sf})}{h_{sf}}$
k_{sm} - saturation constant, Second Year males	bears	$1.2222 * 10^4$	$\frac{(10000)*(1-h_{sm})}{h_{sm}}$
k_{tf} - saturation constant, Third year females	bears	190,000	$\frac{(10000)*(1-h_{tf})}{h_{tf}}$
k_{tm} - saturation constant, Third year males	bears	$2.3333 * 10^4$	$\frac{(10000)*(1-h_{tm})}{h_{tm}}$
k_{af} - saturation constant, Adult females	bears	$6.6923 * 10^4$	$\frac{(10000)*(1-h_{df})}{h_{df}}$
k_{am} - saturation constant, Adult males	bears	$4.2632 * 10^4$	$\frac{(10000)*(1-h_{dm})}{h_{dm}}$

Table A.4: Parameters - Population Proportions and Saturation Constants