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MATHEMATICAL MODELING OF OPTIMAL SEASONAL REPRODUCTIVE STRATEGIES OF PLANT POPULATIONS AND A COMPARISON OF LONG-TERM VIABILITIES OF ANNUALS AND PERENNIALS

by

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In 1954, Lamont Cole posed a question which has motivated much ecological work in the past 50 years: When is the life history strategy of semelparity (organisms reproduce once, then die) favored, via evolution, over iteroparity (organisms may reproduce multiple times in their lifetime)? Although common sense should dictate that iteroparity would always be favored, we can observe that this is not always the case, since annual plants are not only prevalent, but can dominate an area. Also, certain plant species may be perennial in one region, but annual in another. Thus, in these areas, certain characteristics must be present which favor annuals. It has been shown, in prior work, that high environmental volatility, a short growing season, and a low survivorship of adult plants for perennials should favor annuals.

In this work, we seek to answer Cole's question by constructing a single-season, continuous-time model which takes random environmental effects into account. Using this model, we derive an optimal reproduction strategy to maximize the expected yield for the following season for both annuals and perennials. Then, assuming that evolutionary forces dictate this strategy be adopted, we repeat the single-season model for multiple seasons to determine, over a long period of time, which of annuals or perennials is more likely to experience growth under various conditions. The goal is to confirm the prior results as well as construct new results with a more general model.

Contents

List of Figures

List of Tables

Chapter 1

Introduction

In 1954, biologist Lamont Cole, in what is now considered a landmark paper in life history ecology ([5]), put forth the issue of semelparous and iteroparous life histories, both terms which he coined. Specifically, why do both iteroparous (organisms which can reproduce repeatedly during their lifetimes) and semelparous (organisms which reproduce once, then die) organisms exist, and, in a given situation, which strategy would be favored via evolution? On one hand, it seems logical that iteroparity would be the dominant strategy for all organisms to adopt, since, surely, an organism that can reproduce repeatedly in its lifetime should easily trump the output of a semelparous organism. Yet, in nature, many semelparous organisms exist and, in some cases, dominate an area. Therefore, Cole proposed, there must be some evolutionary advantage to being semelparous in certain situations. Since we will be discussing plant reproductive strategies in this work, and annual plants and perennial plants are examples of semelparous and iteroparous organisms, respectively, from here on, we simply use the terms "annuals" and "perennials" to describe the two different reproductive behaviors.

The following statement, known today as "Cole's Paradox," summarizes the highest advantage perennials can have over annuals ([5, p. 118]): "For an annual species, the [maximal] gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size." This maximal gain was derived by assuming that reproduction takes place once every year, perennials can reproduce in their first year of existence, and the perennials produce a fixed number of offspring per year indefinitely with no mortality. So, if the average litter size for annuals is quite high, gaining only one individual per litter would make little difference. Further, since gaining one individual per litter is the *maximal* gain, it seems to make more practical sense for annuals to instead attempt to increase their average litter size rather than switch to being perennials, which would then require that they adapt to surviving over multiple seasons. The "paradox" is that the statement goes against common sense: it almost implies that perennials have an evolutionary disadvantage. However, assuming all traits are the same for both annuals and perennials, Cole then went on to conclude that perennials do have the evolutionary advantage if they have a small average litter size and/or relatively young maturation age ([5, pp. 119-126]).

The most direct extensions of Cole's work that followed were by Charnoff and Schaffer ([3]) in 1973, Truman Young ([29]) in 1981, and Iwasa and Cohen ([14]) in 1989. Charnoff and Schaffer's key result, essentially a "correction" of Cole's key result, is as follows ([3, p. 792]): "For an annual species, the [maximal] gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding P/C to the average litter size," where P is the average adult survivorship, and C is the average juvenile survivorship.

Young further generalized Charnoff and Schaffer's result to include more parameters; for example, time between reproductive episodes and senescence (age where reproduction can no longer occur) for perennials. Not only does he show that, under certain parameter conditions, Cole's and Charnoff/Shaffer's results are special cases of his model, but he shows that perennials are favored when the age of senescence, adult survivorship, and the ratio of prereproductive development time to the time between reproductive episodes are high. On the other hand, annuals are favored when the population growth rate and juvenile survivorship are high ([29, pp. 28-34]).

Iwasa and Cohen, on the other hand, formulate a model independent of Cole's original model. Their model allocates energy proportionally to either a vegetative part of the plant or a storage part, which includes both reproductive organs and material necessary to rebuild the vegetative part of the plant during the next season. Unlike the previously-mentioned models, however, the dynamics within a season are assumed to occur in continuous time (the previous models occur in discrete time). In the process of deriving an optimal energy allocation during a given season, they also discuss that annuals will be favored over perennials if the season length is short, storage efficiency is low, and/or the chances of catastrophic disturbances are high ([14, p. 491]).

Although these models, especially Cole's, have led to some intriguing work and results on the question of annuals vs. perennials by numerous biologists, mainly case studies (see, for example, [4], [8], [11], and [30]), all of the aforementioned models are deterministic. Since natural processes occur continuously, and environmental effects are not wholly deterministic, we wish to extend these ideas by including continuous-time dynamics in each season as well as environmental stochasticity. Also, all of these models assume that reproductive output per season is known a priori; however, evolutionary forces over time have dictated what an optimal reproductive strategy should be for the plants. So, we would also like to see, especially with randomness from the environment, what the effects of the environment and other parameters are on an optimal reproductive strategy. Thus, in this work, we seek to answer the following questions: "In a random environment, assuming each season is measured in continuous time, what reproductive strategy should annuals or perennials adopt in order to maximize their expected yield for the following season? Further, if this is done over multiple seasons, do annuals or perennials have the evolutionary advantage?"

The way that we will incorporate environmental stochasticity and continuous-time dynamics is by way of a stochastic differential equation (SDE). The general form of SDE (and most common in practice) that we will use is the following:

$$dX_t = f(t, X_t)dt + g(t, X_t)dB_t.$$

Here, dB_t represents a small increment of Standard Brownian Motion, which we will call B_t (it is also common to call it W_t since another common name is the Wiener process; according to [16, p. 76], Wiener formalized the mathematical properties of Standard Brownian Motion in 1923); this is a random process which has the following properties (see, for example, [10, pp. 330-332]):

1. $B_0 = 0$.
2. If $0 \leq s < t$, then $B_t - B_s$ is normally distributed with mean 0 and variance $t - s$.
3. If $0 \leq s_1 < s_2 \leq t_1 < t_2$, then $B_{t_2} - B_{t_1}$ and $B_{s_2} - B_{s_1}$ are independent.
4. B_t is continuous almost surely (that is, with probability 1) for all $t \geq 0$.

The SDE can thus be broken up into two terms on the right hand side: a deterministic term, $f(t, X_t)dt$, and a random (stochastic) term, $g(t, X_t)dB_t$. The name "deterministic term" comes from the fact that, if $g(t, X_t) = 0$, then the equation would reduce to a deterministic ordinary differential equation (ODE). Thus, an SDE can roughly be thought of as adding randomness to an ODE.

SDEs have been in existence for many years; as Jarrow and Protter discuss in [16], the first known SDE, which was of the form stated previously, was studied by Kiyosi Ito starting in 1945, culminating in the now-fundamental Ito's Lemma (or Ito's Formula) in 1951 ([16, p. 78]). Ito's Lemma provides a method for constructing a solution to an SDE, but, more fundamentally, defines how to compute an integral of the form

$$\int_0^T f(X_t)dB_t,$$

where X_t may be a random process. His work was later extended by Doob in 1953, Girsanov in the 1950s and 1960, who proved a famous theorem on transformations of Brownian Motion, Meyer in 1962, Courrege in 1963, and Kunita and Watanabe in 1967 ([16, pp. 79-80, 83-85]). For our purposes, however, Ito's Formula will be all we need to analyze the SDE in the model for our plant population.

Not surprisingly, since the real world is not wholly deterministic, numerous ecological papers exist which include randomness in their models. One good example is a paper by Lande ([19]), who discusses population extinction from the standpoints of demographic stochasticity (the growth rate is random) as well as environmental stochasticity and random catastrophes (large, infrequent changes in the population). Another example is a paper by Iwasa and Kubo ([15]), who discuss the optimal reproduction strategy of plants when random environmental effects occur that can either destroy only the vegetative part of a plant, which can be regenerated, or kill the plant altogether. These papers do not involve SDEs, instead relying on other results to change the stochastic problems into deterministic ones for analytical purposes. However, a great resource for biological SDEs is a 2007 book by Edward Allen ([1, pp. 135-153]); he indicates both a general modeling setup for problems involving interacting populations as well as more specific examples (epidemiology and predatorprey dynamics, for instance), discussing both demographic as well as environmental stochasticity. That being said, due to the necessity to solve many SDEs numerically and the fact that theoretical work usually requires measure theory and advanced probability theory, something usually not required for ODEs, it is also not surprising that SDEs are not more prevalent in the literature.

In order to determine what reproductive strategy for a single season will optimize the expected yield for the plants for the following season, we will use techniques from stochastic optimal control theory. Optimal control theory involves choosing a function in order to either maximize or minimize a given functional, subject to differential equation constraints. Many examples of these types of problems are in [20], including many biological problems such as determining an optimal vaccination schedule for an epidemic ([20, pp. 117-122]) and minimizing the impact of an invasive plant species ([20, pp. 201-202, 205-209]).

However, the inspiration for the use of control theory to solve our problem actually did not come from biology; instead, it came from finance. Dai et al ([7]) propose a model for pricing a financial instrument known as a guaranteed minimum withdrawal benefit (GMWB); the basic premise is that an investor pays money to an insurance company, which invests the money in some risky portfolio on his/her behalf. The investor, who is out to maximize his/her profits, must decide whether to ride out his/her entire investment contract (the insurance company is “guaranteed” to pay back the entire amount invested over an agreed-upon period of time) or to withdraw early and face an early withdrawal penalty. Besides the risk of the market, the investor also pays a commission to the insurance company; this also plays a role on the withdrawal strategy. Although the biological scenario we will model is not quite like this, since the “investors” are not playing against anyone else, but rather against the environment, which has no stake in the outcome, the setup of the model and the analysis techniques are inspired by the work done in this paper. In fact, we will also present a possible financial interpretation of the biological model.

Although optimal control theory has been in existence for a long time, the theorems needed to prove optimality of controls for stochastic systems (that is, where the constraints are SDEs) did not arise until the 1990s. In deterministic optimal control theory, one of the most common techniques used to prove optimality is the *Pontryagin Maximum Principle*, discovered by Lev Pontryagin in 1962 ([24]). An extension of this to stochastic optimal control problems was proved by Peng in 1990 ([23]), who proved a necessary condition for optimality, and Zhou in 1996 ([27]), who turned Peng's condition into a sufficient condition.

Keeping all of this in mind, in the following chapters, we will form the model, which will be an optimal control problem, solve the optimal control problem to find optimal reproductive strategies for both annuals and perennials, and then, using these optimal strategies, see what happens to the populations over multiple seasons to determine whether perennials or annuals are more likely to thrive under different conditions. More specifically, here is a rough outline of the work we will perform to answer the posed questions:

- Chapter 2 sets up the model for choosing a reproductive strategy to maximize expected yield for the following season. This is followed by an explanation of a possible financial interpretation of the model.

- Chapter 3 finds an optimal reproductive strategy in the absence of environmental stochasticity. It turns out that, for both annuals and perennials, the optimal strategy is either to not reproduce initially and then, at some designated time during the season, begin reproduction at maximum capacity, or reproduce at maximum capacity all season long. We also discuss when season-long reproduction will be optimal in Section 3.4.

- Chapter 4 finds an optimal reproductive strategy when considering environmental stochasticity. We show that the environment will have no effect on the choice of strategy; that is, the optimal controls found in Chapter 3 will still be optimal.

- Chapter 5 takes the optimal controls discovered in Chapters 3 and 4, assumes the plants follow those strategies and all parameters remain the same over multiple seasons, and then investigates what happens with both annuals and perennials over multiple seasons, first individually, and then comparatively. This investigation seeks to answer the question that Cole initially posed: “When is semelparity more advantageous over iteroparity?”

- Chapter 6 provides some numerical simulation data to not only confirm results from Chapters 3 and 4, but also to see how accurate results from Chapter 5 are in predicting long-term behavior of the plants. As an endnote, we also consider logistic growth and compare results with exponential growth, which will be assumed in the model derived in Chapter 2.

- Chapter 7 summarizes all of the work done and provides indications for what can and, in some cases, should be done in the future to extend the results.

- Two appendices are also present; the first simply details the programs used to run the simulations in Chapter 6, and the second involves an error analysis on some of the work done in Chapter 5.

Chapter 2

Ecological Situation and Model

2.1 The Model and Assumptions

We now present a model for a plant species and its choice of reproduction strategy in order to ensure optimal yield for the following season. This type of model has assumptions and consequences like those in finance; in fact, we will discuss a financial analog to this model in the next section.

Consider a local population (by "local," we mean a portion of the population located in a region where the environmental effects on the population are the same) of a plant species which initially has known adult biomass $W_0 > 0$ and no juveniles or unsprouted reproductive biomass (a general term to mean any biomass which can be spread and sprout into new plants; for example, seeds) at the start of a season, defined as time $t = 0$. The population's goal is to maximize the amount of expected total adult biomass available at the start of next season; that is, the adult biomass left at the end of the season which is expected to survive to next season along with the expected biomass resulting from surviving and sprouting reproductive biomass into adults for next season, defined as time $t = T$. The plants, as a population, "choose" (that is, we assume evolutionary forces will favor those plants which adopt optimal reproductive strategies) how much energy to devote to reproduction, and this will result in some amount of reproductive biomass being produced. However, as we assume that there are environmental effects acting on the population, we assume any energy used for reproductive purposes (that is, adult biomass which is converted to reproductive biomass) becomes "safe." That is, it is no longer at risk of being lost at the hands of the environment, but it is also no longer able to grow in size during the current season, and there is the potential of the reproductive biomass not growing into adult plants. We also assume that "energy" and "biomass" are interchangeable; this makes sense because, as an organism uses energy, it generally loses biomass (think of humans who exercise and lose weight). Thus, to keep things simple, we assume that the loss of biomass is proportional to the loss of energy; further, without loss of generality, we can assume that both are the same measure (we could just appropriately scale the biomass).

For this model, we assume that the adult biomass during the season will be governed by a Geometric Brownian Motion; in other words, calling W_t the adult biomass at time t, $0 \leq t \leq T$,

$$dW_t = rW_t dt + \sigma W_t dB_t, \tag{2.1}$$

where r is the (exponential) growth rate of the population in absence of environmental effects, σ is the volatility of the environment, or how "wild" swings in the environmental effects are expected to be, and B_t is a Standard Brownian Motion. This says that the environmental effects, which we are taking here to be an aggregate of all external factors on the plants' growth, such as temperature, rainfall, disease, and predation, are essentially "white noise." These will influence the overall growth, both positively and negatively.

Likewise, we assume that the plants follow an energy allocation rule similar to the κ rule for energy allocation (discussed in [21]); that is, at any time, the proportion of biomass used for reproduction cannot exceed κ. Whatever proportion is remaining, which is at least $1-\kappa$, is then used for somatic maintenance. For this model, we will assume $0 < \kappa < 1 + r$ is constant over time. Assuming that both the growth and reproduction occur instantaneously and simultaneously, then $\kappa = 1 + r$ would represent the plants using all of their deterministic growth and whatever existed previously for reproduction. Since the stochastic term has mean 0, and is random, then we assume that this maximum value for κ is based solely on the deterministic growth. Because of this, the population cannot use all of its biomass for reproduction in a given instant; however, it can decide to reproduce continuously throughout the season if that ends up being the optimal strategy. This is a logical assumption to make since, even if the plants decide to focus solely on reproduction, they still have to have a vegetative structure in order to create the reproductive biomass. Also, we assume that the plants can begin or end reproduction at any time during the season, which is certainly reasonable because most mature organisms can choose to begin or stop reproduction whenever they want.

With this, we define $\gamma(t)$ to be the (measurable) function which gives the proportion of available adult biomass per unit time which is converted to reproductive biomass at time t. This will be the control function, or strategy, for this model. In reality, γ may also be dependent on W_t; however, for simplicity, we assume that it is solely dependent on t for this model. By assumption, $0 \leq \gamma(t) \leq \kappa$ for all $0 \leq t \leq T$. We will also assume that, once the population begins to convert biomass to reproductive biomass, the conversion is done instantaneously, and it cannot be stored for multiple seasons; once reproductive biomass has been created, it will either sprout into adult plants next season or die.

So, combining this with (2.1), we have that, at time t,

$$dW_t = rW_t dt + \sigma W_t dB_t - \gamma(t) W_t dt.$$

Of course, this equation only holds if $W_t > 0$; if $W_{t_0} = 0$ at any time $0 \leq t_0 < T$, then for all $t_0 \leq t \leq T$, it will remain 0 since, if there is no adult biomass at any instant, there can't be any until next season when the reproductive biomass sprouts.

The goal for the population is to maximize its expected yield for next season, so we next focus on how to represent this. We first define the following parameters:

a = average survivorship of adult plants from the end of the current season to the beginning of the next

ϵ = average proportion of reproductive biomass which sprouts to full-grown adults in the next season

u = average number of times more biomass a full-grown adult has than the reproductive biomass needed for a new plant.

As their definitions suggest, we assume all of these parameters are constant. Note that, if $a = 0$, then we define the plants to be annuals; otherwise, they are defined to be perennials. These definitions are solely based on whether any adults can survive for multiple seasons or not; however, we will show that the reproductive behavior of the plants in each case corresponds to the observed reproductive behaviors of these types of plants. Also, $u > 1$ by definition.

We thus want to maximize the following:

$$E\left[aW_T + \epsilon u \int_0^T \gamma(t)W_t dt\right].$$

The term aW_T represents the adult biomass the population will start with next season leftover from the current season, while the integral term represents the expected adult biomass that seeds planted during the current season will yield next season. The integral is just adding up all of the biomass that is converted to seeds over the course of the season, and the multiplier ϵu accounts for what proportion of those seeds are expected to survive to be full-grown adults, and then how much adult biomass the surviving (and sprouting) seeds will contribute to the population (on average) during the next season. This can be thought of as the "reproductive utility factor."

It is important to note that the reproductive biomass that does sprout into adults is assumed, for the purposes of this model, to be full-grown adults at the very beginning of the next season. Thus, we assume that the season begins once all sprouting biomass has grown into adults.

We can summarize all of this into the following optimization problem, which states that the goal for the plants is to maximize their expected yield for next season while being subjected to both deterministic and stochastic effects:

$$\text{Maximize} \quad E\left[aW_T + b\int_0^T \gamma(t)W_t dt\right] \tag{2.2}$$

$$\text{subject to} \quad dW_t = (r - \gamma(t))W_t dt + \sigma W_t dB_t \tag{2.3}$$

$$W_t \geq 0, \tag{2.4}$$

where $b = \epsilon u$. The change in notation is made because, in the analysis of this model, these two parameters are always together as a product. Also, if $W_{t_0} = 0$ for any time

$0 \leq t_0 < T$, then $W_t = 0$ for all $t \geq t_0$. This practical assumption is clear, and hence it will be omitted from future discussion unless necessary.

Since the reproduction strategy, $\gamma(t)$, is "chosen" by the population, it is natural to turn to methods from control theory to try to solve this problem. In fact, this optimization problem can be solved by a specific control theory method; namely, the *Pontryagin Maximum Principle.* This will be explored in future sections.

2.2 A Financial Analog

Although the model just constructed is going to be used to solve an ecological problem, we note that there is a quite convenient financial interpretation of the model.

Consider an investor whose goal is, by the end of some period of time, to maximize his/her investment. In response, he/she decides to invest his/her money in a risky portfolio, but also has the option to withdraw certain portions of it to be placed in a savings account which has no risk involved and earns some rate of interest. This will be paid based on the balance in the account at the end of the investment period. We assume that any money taken out of the portfolio cannot be put back into it, and no additional money will be introduced into neither the portfolio nor the savings account during the investment period.

We also assume the standard financial assumption that the value of the risky portfolio follows a Geometric Brownian Motion (2.1). Then, money is taken out of the portfolio and put into the savings account at rate $\gamma(t)$, where $0 \leq t \leq T$, and $\gamma(t)$ is the chosen withdrawal rate by the investor at time t. Further, suppose that the investor is not allowed to make excessive withdrawals from the portfolio at any time without paying a penalty. Assuming that this penalty is harsh enough to discourage any thought of incurring it, we can think of this as the "somatic maintenance" requirement for the portfolio, thus requiring $\gamma(t)$ to be less than or equal to some constant rate κ for any time t.

In this case, the quantity $u - 1$ represents the simple interest rate the savings account will earn on its ending balance, and hence, practically, $u \geq 1$, but one would expect u to be relatively close to 1 (otherwise, the bank could lose a lot of money!). ϵ represents how much of each dollar taken from the portfolio and put in the savings account can be kept after any possible transfer fees (we'll assume the transfer fee is a constant proportion of each transaction). So, $0 < \epsilon \leq 1$; if $\epsilon = 1$, then there are no transfer fees. Also, $1 - a$ represents the broker's fee on the balance of the portfolio at the end of the investment period; so, other than on transfers (unless $\epsilon = 1$), this is the only other time the broker collects money in this scenario. Unlike in the biological model, however, where a can feasibly be 0, it doesn't make sense in this interpretation to have a be close to 0, since no rational investor would invest with a broker who will collect almost all, or all, of the money in the risky portfolio at the end of the investment, especially if the investor can't pull all money out at once! It also doesn't make sense to have a equal to 1 since the broker would make no money off the risky portfolio. So, in this financial model, we will assume that a is close to, but *not* equal to, 1.

Thus, we can use the same set of equations as in the biological model, with the following changes in interpretation for the variables and parameters:

$t =$ time

$T =$ length of time of investment

$W_t =$ value of portfolio at time t

$\gamma(t) =$ rate which money is placed into savings account from portfolio at time t

$\kappa =$ maximum withdrawal rate which can occur at time t without penalty

$r =$ riskless interest rate compounded continuously

$\sigma =$ volatility of risky portfolio

$a =$ proportion of money left in portfolio kept after end-of-period broker's fees

$\epsilon =$ proportion of money transferred to savings account kept after transaction fees

$u =$ value of \$1 with simple interest earned on savings account at end of period.

Because the mathematical analysis of this model is the same as that of the ecological model, we will focus solely on the ecological model for the remainder of this work. However, the interested reader may reinterpret the findings in this financial setting if he/she finds it more convenient or interesting.

Remark: Practically, the "somatic maintenance" requirement would most likely be given as a minimal dollar amount which must be in the portfolio at all times during the investment. However, for purposes of having a direct analog between the ecological and financial situations, we stated this requirement as a maximal withdrawal rate at any time t.

Chapter 3

The Deterministic Case

3.1 Finding an Optimal Strategy

We now analyze the ecological model derived in Chapter 2 in the absence of random environmental effects (that is, $\sigma = 0$). To do so, we solve the following optimization problem:

$$\begin{aligned} \text{Maximize} \quad & aW_T + b\int_0^T \gamma(t)W_t dt && (3.1) \\ \text{subject to} \quad & \frac{dW_t}{dt} = (r - \gamma(t))W_t && (3.2) \\ & W_t \geq 0. && (3.3) \end{aligned}$$

Constraint (3.2) comes from dropping the stochastic term in (2.3) and, since we are assuming continuous time, then (3.2) becomes a first-order linear differential equation for W_t. We also note that, since all of the functions are deterministic, then

$$E\left[aW_T + b\int_0^T \gamma(t)W_t dt\right] = aW_T + b\int_0^T \gamma(t)W_t dt.$$

Noting that $W_0 > 0$ is a given constant, then it can be easily verified that

$$W_t = W_0 \cdot \exp\left(rt - \int_0^t \gamma(s)ds\right).$$

Since this holds for all $0 \le t \le T$, we note that (3.3) is clearly satisfied since $W_0 > 0$. Thus, it is redundant, and hence we'll no longer consider it in our analysis. We also note that the value of the objective function is

$$\begin{aligned} aW_T + b\int_0^T \gamma(t)W_t dt = {} & aW_0 \cdot \exp\left(rT - \int_0^T \gamma(t)dt\right) \\ & + bW_0 \int_0^T \gamma(t) \cdot \exp\left(rt - \int_0^t \gamma(s)ds\right) dt. \end{aligned}$$

To find a $\gamma(t)$ which will maximize the objective function, we need some necessary and sufficient conditions for optimality. In order to do this, however, we need some definitions and assumptions.

So, consider the following general optimization problem for $(t, x) \in [0, T] \times G$, where $G \subseteq \mathbb{R}$ and $W_0 \in G$ is given:

$$\begin{aligned} \text{Maximize} \quad & K(W_T) + \int_0^T F(t, W_t, \gamma(t))dt && (3.4) \\ \text{subject to} \quad & \frac{dW_t}{dt} = c(t, W_t, \gamma(t)). && (3.5) \end{aligned}$$

We define U to be the separable metric space (with metric d), which is also a convex set with nonempty interior, which gives the range of the control functions $\gamma(t) \in M$. Here, M is the set of all measurable Markov controls $\gamma(t)$ (that is, the value of $\gamma(t)$ for any $t \in [0, T]$ has no dependence on the value of $\gamma(s)$ for any $s < t$) such that $\gamma(t) \in U$ for all $t \in [0, T]$.

We further assume that $K(x), F(t, x, v), c(t, x, v)$ are:

- measurable
- continuously differentiable with respect to x
- such that there exists a constant $N > 0$ such that, for any choice of x,

  $$|\phi(t, x, v)| \leq N(1 + |x|),$$

  where ϕ is any one of K, F, c, or any of their partial derivatives with respect to x
- such that there is a constant $L > 0$ and a "modulus of continuity" $\omega : [0, \infty) \rightarrow [0, \infty)$ such that, taking ϕ to be any of K, F, c,

  $$\begin{aligned} |\phi(t, x, v) - \phi(t, x^*, v^*)| &\leq L|x - x^*| + \omega(d(v, v^*)) \\ \left| \frac{\partial \phi}{\partial x}(t, x, v) - \frac{\partial \phi}{\partial x}(t, x^*, v^*) \right| &\leq \omega(|x - x^*| + d(v, v^*)) \end{aligned}$$

  for all $t \in [0, T]$, $x, x^* \in G$, $v, v^* \in U$
- such that c, F are locally Lipschitz with respect to v

We also require that, for any $W_0 \in G$, any choice of $\gamma(t) \in M$ implies $W_t \in G$ for all $t \in [0, T]$; that is, all possible controls are admissible. Since these will be the standard assumptions for (3.4-3.5), we will call this list (DA) for "deterministic assumptions." So, (DA) implies that any choice of $\gamma(t)$ will lead to a unique solution W_t of (3.5) (see, for example, Theorem 8.13 in [18, pp. 340-342]).

Once $\gamma(t)$, and hence W_t, is chosen, we define the *adjoint function* $p(t)$ to be the function satisfying the following:

$$p'(t) = -\left(\frac{\partial c}{\partial x}(t, W_t, \gamma(t))p(t) + \frac{\partial F}{\partial x}(t, W_t, \gamma(t))\right)$$
$$p(T) = \frac{\partial K}{\partial x}(W_T).$$

If (3.4-3.5) satisfies (DA), then there is a unique adjoint function for a given $\gamma(t)$ and W_t.

From this, we then define the following function:

$$H(t, x, v, p) = p(t)c(t, x, v) + F(t, x, v).$$

This is called the *Hamiltonian* for (3.1-3.3). It will play an important role in our necessary and sufficient conditions for optimality, which we are now ready to state. We begin with a necessary condition, which is Theorem 2.1 in Yong-Zhou (also called the *Pontryagin Maximum Principle*) ([27, p. 103]):

Theorem 3.1: Assume (3.4-3.5) satisfies (DA). If $\gamma^*(t)$ is an optimal control with corresponding constraint solution W_t^* and adjoint function $p(t)$, then

$$H(t, W^*(t), \gamma^*(t), p(t)) = \max_{v \in U} H(t, W^*(t), v, p(t))$$

for almost every $t \in [0, T]$.

Proof: A proof can be found in [27, pp. 104-106].

Next, we give a sufficient condition for optimality:

Theorem 3.2: Assume (3.4-3.5) satisfies (DA). Let $\gamma^*(t) \in M$, W_t^* be the corresponding constraint solution, and $p(t)$ be the corresponding adjoint function. If:

1. K is concave

2. For any other choice of $\gamma(t) \in M$ and corresponding W_t,

$$H(t, W_t, \gamma(t), p(t)) - H(t, W_t^*, \gamma^*(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t^*, \gamma^*(t), p(t)) \cdot (W_t - W_t^*)$$

   for all $t \in [0, T]$

then $\gamma^*(t)$ is an optimal control.

Proof: We begin by defining $\xi(t) = W_t - W_t^*$. By assumption, $\xi(t)$ satisfies

$$\begin{aligned} \xi'(t) &= \frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + \alpha(t) \\ \xi(0) &= 0, \end{aligned}$$

where

$$\alpha(t) = -\frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + c(t, W_t, \gamma(t)) - c(t, W_t^*, \gamma^*(t)).$$

With this in mind, along with the given assumptions, we have the following:

$$\begin{aligned}
\frac{\partial K}{\partial x}(W_T^*)\cdot\xi(T) &= p(T)\xi(T) - p(0)\xi(0)\\
&= \int_0^T \left(-\left(\frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot p(t) + \frac{\partial F}{\partial x}(t, W_t^*, \gamma^*(t)) \right) \xi(t) \right.\\
&\qquad \left. + p(t) \left(\frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + \alpha(t) \right) \right) dt\\
&= \int_0^T \left(-\frac{\partial F}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + p(t)\alpha(t) \right) dt\\
&= \int_0^T \left(\left(-\frac{\partial H}{\partial x}(t, W_t^*, \gamma^*(t), p(t)) + p(t)\frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \right) \xi(t) \right.\\
&\qquad \left. + p(t)\alpha(t) \right) dt\\
&= \int_0^T \left(-\frac{\partial H}{\partial x}(t, W_t^*, \gamma^*(t), p(t)) \cdot (W_t - W_t^*) \right.\\
&\qquad \left. + p(t)(c(t, W_t, \gamma(t)) - c(t, W_t^*, \gamma^*(t))) \right) dt\\
&\le \int_0^T (H(t, W_t^*, \gamma^*(t), p(t)) - H(t, W_t, \gamma(t), p(t))\\
&\qquad + p(t)(c(t, W_t, \gamma(t)) - c(t, W_t^*, \gamma^*(t)))) \, dt\\
&= \int_0^T (F(t, W^*(t), \gamma^*(t)) - F(t, W_t, \gamma(t))) \, dt.
\end{aligned}$$

Since $K(x)$ is assumed concave and $C^1(G)$, then

$$K(W_T) - K(W_T^*) \le \frac{\partial K}{\partial x}(W_T^*) \cdot (W_T - W_T^*).$$

Tying this all together, we then have

$$K(W_T) + \int_0^T f(t, W_t, \gamma(t))dt \le K(W_T^*) + \int_0^T f(t, W_t^*, \gamma^*(t))dt.$$

Since $\gamma(t) \in M$ was arbitrary, this completes the proof of Theorem 3.2.

Remark 1: This theorem and proof is based on Theorem 2.5 in [27, pp. 112-113]. The key difference between their theorem and our Theorem 3.2 is that the Hamiltonian ($H(t, x, u, p)$) is assumed concave with respect to x, u. Their sufficient condition involves showing that, for almost every $t \in [0, T]$,

$$H(t, W^*(t), \gamma^*(t), p(t)) = \max_{v \in U} H(t, W^*(t), v, p(t)).$$

If this and concavity of H is assumed, then the condition on H used in Theorem 3.2 can be derived, leading to a virtually identical proof, and turning Theorem 3.1 into an if-and-only-if statement. However, as we'll soon show, the Hamiltonian for our problem is not concave, and hence a different sufficient condition is needed.

Remark 2: In general, if an optimal $\gamma^*(t)$ exists, it is not necessarily unique. For our model, however, we will be able to show that an optimal $\gamma^*(t)$ is essentially unique; that is, except for possibly at one point, $\gamma^*(t)$ is unique.

We now go back to our model and analyze it with this framework. First, we note that $G = [0, \infty)$ and $U = [0, \kappa]$ (giving U the metric $|\cdot|$ results in U being convex with nonempty interior and a separable metric space) for (3.1-3.3). Since

$$\begin{aligned} c(t, x, v) &= (r - v)x \\ F(t, x, v) &= bxv \\ K(x) &= ax, \end{aligned}$$

these all clearly satisfy (DA) (in fact, c, F are actually Lipschitz with respect to v since they are linear in v). Further, we can define the adjoint variable for a given $\gamma(t) \in M$ and corresponding W_t (M is the set of all measurable Markov controls $\gamma(t)$

such that $0 \leq \gamma(t) \leq \kappa$ for all $t \in [0, T]$) as follows:

$$\begin{aligned} p'(t) &= (\gamma(t) - r)p(t) - b\gamma(t) \\ p(T) &= a. \end{aligned}$$

Once this is solved, then we can define the Hamiltonian for (3.1-3.3) as follows:

$$\begin{aligned} H(t, W_t, \gamma(t), p(t)) &= p(t)(r - \gamma(t))W_t + bW_t\gamma(t) \\ &= W_t \cdot (rp(t) + \gamma(t)(b - p(t))). \end{aligned}$$

Since $K(x) = ax$ is clearly concave (it is linear), then our goal will be to find a $\gamma^*(t)$ which results in the conditions on H from Theorems 3.1 and 3.2 being satisfied. The following sections focus on this in two cases: when $a = 0$ (annuals) and when $a > 0$ (perennials). Recall these definitions come from whether all of the adults in the population will die at the end of the season, or some of them will survive into the next season, respectively.

3.2 Annuals

We now solve the problem in the deterministic case assuming that the plants are annuals ($a = 0$). First, however, since $a = 0$ here, we note that, in this case, the objective function becomes simplified. Hence, here, we wish to maximize

$$b\int_0^T \gamma(t)W_t dt.$$

Recalling that

$$W_t = W_0 \cdot \exp\left(rt - \int_0^t \gamma(s)ds\right), \tag{3.6}$$

then we wish to maximize

$$bW_0 \int_0^T \gamma(t) \cdot \exp\left(rt - \int_0^t \gamma(s)ds\right) dt. \tag{3.7}$$

To construct a possible candidate for an optimal control, which we'll refer to as $\gamma^*(t)$, consider the reproductive behavior of annual plants. By definition, annual plants grow, reproduce once, and then die at the end of the reproductive period. Thus, it makes sense that an optimal strategy would be to have the plants initially not allocating any energy to reproduction, instead focusing on the growth and preservation of the existing adults. Then, at some time during the season, the plants "turn on" full reproduction until the season ends, at which point all of the adult biomass will die off. The "turn-off, turn-on" strategy seems to also be indicated by the Hamiltonian, since

$$H(t, W_t, \gamma(t), p(t)) = W_t \cdot (rp(t) + \gamma(t)(b - p(t))).$$

Theorem 3.1 tells us, since $W_t \geq 0$, that an optimal $\gamma(t)$ can only take on two values on $[0, T]$: 0 or κ, depending on the sign of $b - p(t)$ (although $\gamma(t)$ can technically be anything if $b = p(t)$, for simplicity, we will assume $\gamma(t) = \kappa$ at these points).

Thus, we will define

$$\gamma(t) = \kappa \bar{H}(t - d_A),$$

where $\bar{H}(x)$ is the Heaviside function with $\bar{H}(0) = 1$, and $d_A = T - \bar{d_A}$, where $\bar{d_A}$ is to be determined. Plugging this $\gamma(t)$ into (3.7) and assuming $r \neq \kappa$ ($r = \kappa$ is a special case which will be analyzed later), we obtain the following:

$$\begin{aligned}
&bW_0 \int_0^T \gamma(t) \exp\left(rt - \int_0^t \gamma(s)ds\right) dt \\
&= bW_0\kappa \int_{d_A}^T \exp\left(rt - \kappa(t - d_A)\right) dt \\
&= \frac{bW_0\kappa}{r-\kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right).
\end{aligned}$$

Next, we will take a derivative of the above with respect to d_A, set it equal to 0, and then solve for d_A to obtain the d_A which maximizes (3.7). This gives us:

$$\begin{aligned}
\frac{bW_0\kappa}{r-\kappa} \left(\kappa \cdot \exp(rT - \kappa(T - d_A)) - r \cdot \exp(rd_A)\right) &= 0 \\
\kappa \cdot \exp(rT - \kappa(T - d_A)) - r \cdot \exp(rd_A) &= 0 \\
\exp(T(r-\kappa)) &= \frac{r}{\kappa} \cdot \exp(d_A(r-\kappa)) \\
T(r-\kappa) - \ln\left(\frac{r}{\kappa}\right) &= d_A(r-\kappa) \\
d_A &= T - \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right).
\end{aligned}$$

If $r = \kappa$, note that the expression for d_A is undefined, meaning that a different expression for the starting time for reproduction is needed; we'll call this d_A^*. So, plugging in $\gamma(t) = \kappa \bar{H}(t - d_A^*)$, where $0 \leq d_A^* \leq T$, into (3.7) obtains

$$\begin{aligned}
&bW_0\kappa \int_{d_A^*}^T \exp\left(\kappa t - \kappa(t - d_A^*)\right) dt \\
&= bW_0\kappa(T - d_A^*) \exp(\kappa d_A^*).
\end{aligned}$$

Taking the derivative of this with respect to d_A^*, setting it equal to 0, and then solving for d_A^* obtains

$$d_A^* = T - \frac{1}{\kappa}.$$

To verify that both d_A and d_A^* are the starting times that maximize (3.7) when choosing $\gamma(t) = \kappa\bar{H}(t-d)$, one can simply use the Second Derivative Test from calculus (see, for example, [25, p. 284]).

Remark: One could also obtain d_A^* by simply noting that

$$\begin{aligned} T - \frac{1}{\kappa} &= T - \frac{d}{d\kappa}\ln(\kappa) \\ &= T - \lim_{r\to\kappa}\frac{\ln(r)-\ln(\kappa)}{r-\kappa} \\ &= T - \lim_{r\to\kappa}\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right). \end{aligned}$$

Since both d_A and d_A^* represent at which time during the season the plants should begin reproducing according to this choice of $\gamma(t)$, it is interesting to note that these times are *not* dependent on b. This is justified because, biologically speaking, the value of b is of much less significance to the annuals' choice to reproduce since they have to reproduce to sustain their population as opposed to perennials. Also, regardless of the values of r, κ, both of these times are less than T (both $r-\kappa$ and $\ln\left(\frac{r}{\kappa}\right)$ have the same sign, and $\frac{1}{\kappa}$ is positive), meaning the annuals will always reproduce; it is just a question of when they will start. Should d_A (or d_A^*) as computed by the above formula be negative, then we will take it to simply be equal to 0 for practicality purposes, meaning that the plants will reproduce all season long; this assumption is justified mathematically in the proof of Theorem 3.3 below. This possibility does exist and will be discussed in Section 3.4.

The next step is to show that $\gamma(t) = \kappa\bar{H}(t-d_A)$ (or $\kappa\bar{H}(t-d_A^*)$) is indeed an optimal choice for a reproductive strategy. To do this, we will first check that the necessary condition (Theorem 3.1) is satisfied, followed by the sufficient condition (Theorem 3.2), which means we need to find the corresponding adjoint function. So, in this case,

$$\begin{aligned} &p'(t) = (\gamma(t) - r)p(t) - b\gamma(t) \\ &p(T) = 0, \end{aligned}$$

which has solution

$$p(t) = b \int_t^T \gamma(s) \cdot \exp\left(r(s-t) - \int_t^s \gamma(u) du \right) ds. \tag{3.8}$$

We then have the following theorem:

Theorem 3.3: If $a = 0$, then $\gamma(t) = \kappa \bar{H}(t - d_A)$ is an optimal control for (3.1-3.3), replacing d_A with d_A^* if $r = \kappa$.

Proof: We begin with the case $r \neq \kappa$. Plugging in $\gamma(t) = \kappa \bar{H}(t - d_A)$ into (3.8) gives us:

$$\begin{aligned} p(t) &= \begin{cases} b\kappa \int_{d_A}^T \exp\left(r(s-t) - \kappa(s - d_A)\right) ds & t < d_A \\ b\kappa \int_t^T \exp\left(r(s-t) - \kappa(s-t)\right) ds & t \geq d_A \end{cases} \\ &= \begin{cases} \frac{b\kappa}{r-\kappa} \left(\exp(r(T-t) - \kappa(T - d_A)) - \exp(r(d_A - t))\right) & t < d_A \\ \frac{b\kappa}{r-\kappa} \left(\exp(r(T-t) - \kappa(T-t)) - 1\right) & t \geq d_A \end{cases}. \end{aligned}$$

Noting that, for this $\gamma(t)$,

$$W_t = \begin{cases} W_0 \cdot \exp(rt) & t < d_A \\ W_0 \cdot \exp(rt - \kappa(t - d_A)) & t \geq d_A \end{cases},$$

we can find the Hamiltonian for this $\gamma(t)$ as follows:

$$\begin{aligned} H(t, W_t, \gamma(t), p(t)) &= W_t \cdot (rp(t) + \gamma(t)(b - p(t))) \\ &= \begin{cases} W_t \cdot (rp(t)) & t < d_A \\ W_t \cdot (rp(t) + \kappa(b - p(t))) & t \geq d_A \end{cases} \\ &= \begin{cases} \frac{W_0 br\kappa}{r-\kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right) & t < d_A \\ \frac{W_0 br\kappa}{r-\kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rt - \kappa(t - d_A))\right) & \\ +W_0\kappa \cdot \exp(rt - \kappa(t - d_A)) & \\ \quad \cdot \big(b - \frac{b\kappa}{r-\kappa} \left(\exp(r(T - t) - \kappa(T - t)) - 1\right)\big) & t \geq d_A \end{cases} \end{aligned}$$

$$H(t, W_t, v, p(t)) = \begin{cases} \frac{W_0 br\kappa}{r-\kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right) & \\ +W_0 v \,(b \cdot \exp(rt) & \\ \qquad -\frac{b\kappa}{r-\kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right)\big) & t < d_A \\ \frac{W_0 br\kappa}{r-\kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rt - \kappa(t - d_A))\right) & \\ +W_0 v \cdot \exp(rt - \kappa(t - d_A)) & \\ \quad \cdot \big(b - \frac{b\kappa}{r-\kappa} \left(\exp(r(T - t) - \kappa(T - t)) - 1\right)\big) & t \geq d_A \end{cases}.$$

We now need to check that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0, \kappa]} H(t, W_t, v, p(t)).$$

To do this, we begin with the branch where $t < d_A$. Here, we note that only one piece is dependent on v in the expression for $H(t, W_t, v, p(t))$; namely,

$$W_0 v\left(b \cdot \exp(rt) - \frac{b\kappa}{r-\kappa}\left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right)\right).$$

We want to show that this is maximized when $v = 0$, or, equivalently,

$$W_0\left(b \cdot \exp(rt) - \frac{b\kappa}{r-\kappa}\left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right)\right) \leq 0 \tag{3.9}$$

for all $t < d_A$. But, we note that the left side of (3.9) clearly strictly increases with respect to t since $W_0, b > 0$, and so it will suffice to verify it when $t = d_A$. So, we plug this value in for t and note that we want to show:

$$\begin{aligned}
W_0\left(b \cdot \exp(rd_A) - \frac{b\kappa}{r-\kappa}\left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right)\right) &\leq 0\\
1 - \frac{\kappa}{r-\kappa}\left(\exp((r-\kappa)(T - d_A)) - 1\right) &\leq 0\\
1 - \frac{\kappa}{r-\kappa}\left(\frac{r}{\kappa} - 1\right) &\leq 0\\
0 &\leq 0
\end{aligned}$$

since $d_A = T - \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)$. Thus, (3.9) holds.

We next look at the branch where $t \geq d_A$. Again, only one piece of $H(t, W_t, v, p(t))$ is dependent on v; namely,

$$W_0 v \cdot \exp(rt - \kappa(t - d_A))\left(b - \frac{b\kappa}{r-\kappa}\left(\exp(r(T-t) - \kappa(T-t)) - 1\right)\right).$$

We want to show that this is maximized when $v = \kappa$, or, equivalently,

$$W_0 \cdot \exp(rt - \kappa(t - d_A)) \left(b - \frac{b\kappa}{r - \kappa} \left(\exp(r(T - t) - \kappa(T - t)) - 1\right) \right) \geq 0. \quad (3.10)$$

Note that the partial derivative with respect to t of the left side of this inequality is

$$W_0 br \cdot \exp(rt - \kappa(t - d_A)),$$

which is positive for all $t \geq d_A$, and hence the left side of (3.10) is strictly increasing, meaning it will again suffice to prove the inequality is true when $t = d_A$. Plugging in $t = d_A$ into the left side of (3.10) yields

$$W_0 \left(b \cdot \exp(rd_A) - \frac{b\kappa}{r - \kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A)\right) \right).$$

We've already shown that this left side is equal to 0 when verifying (3.9), and hence (3.10) holds. Thus, indeed, we have shown

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

Finally, we need to check that the sufficient condition, Theorem 3.2, holds. So, let $\bar{\gamma}(t) \in M$ be some other control with $\bar{W}_t$ the corresponding constraint solution. Then,

$$\begin{aligned} &H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \\ &= (\bar{W}_t - W_t)(rp(t)) + (\bar{W}_t \cdot \bar{\gamma}(t) - W_t \cdot \gamma(t))(b - p(t)) \end{aligned}$$

and

$$\frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t)) \cdot (\bar{W}_t - W_t) = (\bar{W}_t - W_t)(rp(t) + \gamma(t)(b - p(t))).$$

So, for Theorem 3.2 to hold, we need to show that

$$\bar{\gamma}(t)(b - p(t)) \leq \gamma(t)(b - p(t)).$$

By the work done previously, we've shown that $b - p(t) < 0$ if $t < d_A$ and $b - p(t) \geq 0$ if $t \geq d_A$. So, the above inequality reduces to

$$\begin{cases} \bar{\gamma}(t) \geq 0 & t < d_A \\ \bar{\gamma}(t) \leq \kappa & t \geq d_A \end{cases}.$$

This is clearly true by definition of M, and hence, for any $\bar{\gamma}(t) \in M$,

$$H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t))$$

for all $t \in [0, T]$. Thus, by Theorem 3.2, $\gamma(t) = \kappa \bar{H}(t - d_A)$ is an optimal control when $r \neq \kappa$. Should the expression for d_A be negative (hence, we'd take $d_A = 0$), then only the branch where t is at least d_A needs to be checked, and the proof is exactly the same to show that, in this case, $\gamma(t) = \kappa$ is an optimal control.

Next, we assume that $r = \kappa$ and proceed in the same way. So, we first plug in

$\gamma(t) = \kappa \bar{H}(t - d_A^*)$ into the formula for $p(t)$ and obtain:

$$p(t) = \begin{cases} b\kappa \int_{d_A^*}^{T} \exp\left(\kappa(s-t) - \kappa(s - d_A^*)\right) ds & t < d_A^* \\ b\kappa \int_{t}^{T} \exp\left(\kappa(s-t) - \kappa(s-t)\right) ds & t \geq d_A^* \end{cases}$$

$$= \begin{cases} b\kappa(T - d_A^*) \exp(\kappa(d_A^* - t)) & t < d_A^* \\ b\kappa(T-t) & t \geq d_A^* \end{cases}.$$

For this $\gamma(t)$,

$$W_t = \begin{cases} W_0 \cdot \exp(\kappa t) & t < d_A^* \\ W_0 \cdot \exp(\kappa d_A^*) & t \geq d_A^* \end{cases},$$

and thus the Hamiltonian is:

$$\begin{aligned} H(t, W_t, \gamma(t), p(t)) &= W_t(\kappa p(t) + \gamma(t)(b - p(t))) \\ &= \begin{cases} W_t \cdot \kappa p(t) & t < d_A^* \\ W_t \cdot \kappa b & t \geq d_A^* \end{cases} \\ &= \begin{cases} W_0 b\kappa (T - d_A^*) \exp(\kappa d_A^*) & t < d_A^* \\ W_0 b\kappa \cdot \exp(\kappa d_A^*) & t \geq d_A^* \end{cases} \\ H(t, W_t, v, p(t)) &= \begin{cases} W_0 b \left(\kappa(T - d_A^*) \exp(\kappa d_A^*)\right. & \\ \quad \left.+ v\left(\exp(\kappa t) - \kappa(T - d_A^*) \exp(\kappa d_A^*)\right)\right) & t < d_A^* \\ W_0 b \exp(\kappa d_A^*) \left(\kappa^2 (T-t) + v(1 - \kappa(T-t))\right) & t \geq d_A^* \end{cases}. \end{aligned}$$

We now need to check that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

Assuming $t < d_A^*$, the only term of $H(t, W_t, v, p(t))$ that depends on v is

$$W_0 bv \left(\exp(\kappa t) - \kappa(T - d_A^*) \exp(\kappa d_A^*)\right).$$

Note that, if $d_A^* > 0$, then $\kappa(T - d_A^*) = 1$. We don't need to be concerned with the case where $d_A^* = 0$ since this branch would be irrelevant in that case. Thus, this expression simplifies to

$$W_0 bv \left(\exp(\kappa t) - \exp(\kappa d_A^*)\right).$$

Since e^x is an increasing function, then this is clearly negative for all $t < d_A^*$, meaning that, to maximize it with respect to $v \in [0, \kappa]$, we need to set $v = 0$.

Next, assuming $t \geq d_A^*$, the only term of $H(t, W_t, v, p(t))$ that depends on v is

$$W_0 bv \cdot \exp(\kappa d_A^*)(1 - \kappa(T - t)).$$

Determining what value of v will maximize this comes down to determining the sign of

$$1 - \kappa(T - t) = 1 + \kappa t - \kappa T.$$

Note that, at $t = T - \frac{1}{\kappa}$, the above is equal to 0. Further, since it clearly increases with respect to t, then this quantity is nonnegative for all $t \geq d_A^*$, and hence, to maximize $H(t, W_t, v, p(t))$ with respect to v when $t \geq d_A^*$, we need to set $v = \kappa$. This, along with the above, proves that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

Now, for sufficiency, we need to check that Theorem 3.2 holds. So, let $\bar{\gamma}(t) \in M$ be some other control with $\bar{W}_t$ the corresponding constraint solution. Then, as before,

$$\begin{aligned} &H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \\ &= (\bar{W}_t - W_t)(\kappa p(t)) + (\bar{W}_t \cdot \bar{\gamma}(t) - W_t \cdot \gamma(t))(b - p(t)) \end{aligned}$$

and

$$\frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t)) \cdot (\bar{W}_t - W_t) = (\bar{W}_t - W_t)(\kappa p(t) + \gamma(t)(b - p(t))).$$

So, for Theorem 3.2 to hold, we need to show that

$$\bar{\gamma}(t)(b - p(t)) \leq \gamma(t)(b - p(t)).$$

Looking at the expression for $p(t)$ in this case, $b - p(t) < 0$ if $t < d_A^*$ and $b - p(t) \geq 0$ if $t \geq d_A^*$. Thus, the above inequality reduces to

$$\begin{cases} \bar{\gamma}(t) \geq 0 & t < d_A^* \\ \bar{\gamma}(t) \leq \kappa & t \geq d_A^* \end{cases}.$$

This is clearly true by definition of M, and hence, for any $\bar{\gamma}(t) \in M$,

$$H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t))$$

for all $t \in [0, T]$. Thus, by Theorem 3.2, $\gamma(t) = \kappa \bar{H}(t - d_A^*)$ is an optimal control when $r = \kappa$. Also, as discussed above, should the expression for d_A^* be negative, we have that $\gamma(t) = \kappa$ is an optimal control. This completes the proof of Theorem 3.3.

Remark 1: Note that $\gamma^*(t) = \kappa \bar{H}(t - d_A)$ (or d_A^* if $r = \kappa$) is an optimal reproduction strategy; however, it is clearly not unique if $d_A > 0$, as one can simply set $\gamma(d_A) = 0$ (or any value in $[0, \kappa]$) and end up with the same value for the objective function as $\gamma^*(t) = \kappa \bar{H}(t - d_A)$ yields. However, except for that one point, we *can* show that $\gamma^*(t)$ is uniquely determined.

To do so, we recall that, given any $\gamma(t) \in M$, the adjoint is:

$$p(t) = b \int_t^T \gamma(s) \cdot \exp\left(r(s-t) - \int_t^s \gamma(u)du \right) ds.$$

Recall that we wish to maximize the Hamiltonian over the image space for controls $[0, \kappa]$; hence, we want to maximize, with respect to v,

$$H(t, W_t, v, p(t)) = W_t \cdot (rp(t) + v(b - p(t))).$$

Maximizing this requires that we choose $v = 0$ if $b < p(t)$ and $v = \kappa$ if $b > p(t)$. So, noting that $p(T) = 0$ by definition, we must have, since $b > 0$, $v = \kappa$ at $t = T$. We work backwards from here to complete this argument.

Plugging $\gamma(t) = \kappa$ into the formula for $p(t)$, we note that, if $\gamma(t) > 0$, then $p(t)$ is continuous and strictly monotone decreasing since the integrand is always positive in this case. Thus, there must be an interval $[t^*, T]$ where $v = \kappa$ to maximize H. But, it is straightforward to check that $p(t) = b$ when $t = T - \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right)$; hence, this is the t^* for the interval where $v = \kappa$.

At that point, continuing to work backwards, we must switch to $v = 0$ since $p(t)$ is strictly monotone decreasing whenever $\gamma(t) > 0$. Thus, except for possibly the point t^* (if $t^* > 0$, that is), $\gamma^*(t) = \kappa \bar{H}(t - d_A)$ is unique.

Remark 2: It is also important to note what the optimal value of the objective function will be in this case. Since we know an optimal control (namely, $\gamma^*(t) =$

$\kappa \bar{H}(t-d_A))$, we simply plug it in to (3.7) to find that the optimal value is

$$\begin{aligned} b\int_0^T \gamma^*(t)W_t dt &= b\kappa W_0 \int_{d_A}^T \exp(rt-\kappa(t-d_A))dt \\ &= \frac{bW_0\kappa}{r-\kappa}\left(\exp(rT-\kappa(T-d_A))-\exp(rd_A)\right) \end{aligned}$$

if $r \neq \kappa$, and

$$b\int_0^T \gamma^*(t)W_t dt = bW_0 \cdot \exp(\kappa d_A^*)$$

if $r = \kappa$ (use d_A^* instead of d_A).

Remark 3: As previously mentioned, using Theorem 3.1 as an if-and-only-if statement won't work here because the Hamiltonian $H(t,x,v,p) = x(rp + v(b-p))$ is not concave with respect to (x,v). To see why, we note that, holding t,p constant, the corresponding Hessian matrix is

$$\begin{pmatrix} \frac{\partial^2 H}{\partial x^2} & \frac{\partial^2 H}{\partial x \partial u} \\ \frac{\partial^2 H}{\partial u \partial x} & \frac{\partial^2 H}{\partial^2 u} \end{pmatrix} = \begin{pmatrix} 0 & b-p \\ b-p & 0 \end{pmatrix}.$$

This matrix has eigenvalues $\lambda = \pm(b-p(t))$, and hence the matrix is not negative semidefinite (that would require $p(t) = b$ for all t, which does not satisfy the ODE for $p(t)$), a necessary and sufficient condition for concavity (see, for example, [9, p. 586]). This is why we needed Theorem 3.2.

Thus, biologically, this optimal strategy says that either, initially, the plants should not reproduce at all and then, at some designated time during the season, reproduce as much as possible until the end of the season, or reproduce all season long. This makes sense because this allows the population to grow for a while in many cases, allowing more resources to be poured into reproduction (and hence allowing for a higher potential population next season), but also giving enough time for the population to reproduce as much as it can. However, depending on the values of r, κ, and T, it may be better for the population to reproduce all season long; we will discuss this scenario in Section 3.4.

3.3 The Deterministic Case (Perennials)

We now solve the problem in the deterministic case assuming that the plants are perennials ($a > 0$). So, recall that we want to maximize:

$$aW_0 \cdot \exp\left(rT - \int_0^T \gamma(t)dt\right) + bW_0 \int_0^T \gamma(t) \cdot \exp\left(rt - \int_0^t \gamma(s)ds\right) dt.$$

We will do this by the same method that we used in the annuals case; namely, trying to find a $\gamma^*(t) \in M$ that satisfies the necessary and sufficient conditions in Theorems 3.1 and 3.2, respectively. In order to do this, we'll have to find the adjoint function; hence, we need to solve:

$$\begin{aligned} p'(t) &= (\gamma(t) - r)p(t) - b\gamma(t) \\ p(T) &= a. \end{aligned}$$

This has solution

$$p(t) = a \cdot \exp\left(r(T-t) - \int_t^T \gamma(s)ds\right) + b \int_t^T \gamma(s) \cdot \exp\left(r(s-t) - \int_t^s \gamma(u)du\right) ds. \tag{3.11}$$

However, unlike the annuals case, there is actually a difference in what the optimal strategy is, depending on the ratio b/a; specifically, if $b/a \leq 1$ or $b/a > 1$. In the case $b/a \leq 1$, we have the following lemma:

Lemma 3.4: If $a > 0$ and $0 < b/a \leq 1$, then $\gamma(t) = 0$ is an optimal control for (3.1-3.3).

Proof: We begin by plugging in $\gamma(t) = 0$ into (3.11), which gives us $p(t) = a \cdot \exp(r(T-t))$.

For this $\gamma(t)$,

$$W_t = W_0 \cdot \exp(rt).$$

We can then find the Hamiltonian for this $\gamma(t)$ as follows:

$$\begin{aligned} H(t, W_t, \gamma(t), p(t)) &= W_t \cdot (rp(t) + \gamma(t)(b - p(t))) \\ &= arW_0 \cdot \exp(rT) \\ H(t, W_t, v, p(t)) &= arW_0 \cdot \exp(rT) + vW_0 \cdot \exp(rt)(b - a \cdot \exp(r(T-t))). \end{aligned}$$

We now need to check that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

To do this, we note that only one term of $H(t, W_t, v, p(t))$ is dependent on v; namely,

$$W_0 v \cdot \exp(rt)(b - a \cdot \exp(r(T-t))).$$

We want to show that this is maximized when $v = 0$, or, equivalently,

$$\begin{aligned} b - a \cdot \exp(r(T-t)) \leq 0 \\ b/a \leq \exp(r(T-t)) \end{aligned}$$

for all $t \in [0, T]$. However, by assumption, $b/a \leq 1$, and, clearly, $\exp(r(T-t)) \geq 1$

for all $t \in [0, T]$, so this inequality is true. So, $H(t, W_t, v, p(t))$ is maximized when $v = 0$, meaning, indeed,

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

Thus, the necessary condition (Theorem 3.1) holds.

Now, we need to check that the sufficient condition (Theorem 3.2) holds. So, let $\bar{\gamma}(t) \in M$ be some other control with $\bar{W}_t$ the corresponding constraint solution. Then,

$$H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) = (\bar{W}_t - W_t)(rp(t)) + (\bar{W}_t \cdot \bar{\gamma}(t) - W_t \cdot \gamma(t))(b - p(t))$$

and

$$\frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t)) \cdot (\bar{W}_t - W_t) = (\bar{W}_t - W_t)(rp(t) + \gamma(t)(b - p(t))).$$

So, for Theorem 3.2 to hold, we need to show that

$$\bar{\gamma}(t)(b - p(t)) \leq 0.$$

By the work done previously, we've already shown that $b - p(t) \leq 0$; hence, for any $\bar{\gamma}(t) \in M$,

$$H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t))$$

for all $t \in [0, T]$. Thus, by Theorem 3.2, $\gamma(t) = 0$ is an optimal control when $b/a \leq 1$, and this completes the proof of Lemma 3.4.

Remark: If we plug in $\gamma^*(t) = 0$ into (3.1), we get the optimal value

$$aW_T + b\int_0^T \gamma^*(t)W_t dt = aW_0 \cdot \exp(rT)$$

in this case.

We note that this strategy of doing nothing in terms of reproduction and focusing on preserving and growing the existing adult biomass when $b/a \leq 1$ certainly makes sense since this implies that the plant population will actually be worse off reproducing than simply growing as is (the tradeoff for a units of adult biomass this season is b units of adult biomass for next season).

Next, if $b/a > 1$, we note that, in this case, there is incentive to reproduce since the tradeoff for one unit of adult biomass this season is more than one unit of adult biomass next season. Taking inspiration from the annuals case, we propose that an optimal reproduction strategy is either to initially do nothing and then turn on maximum reproduction at some time in the future until the end of the season, or to simply have maximum reproduction going all season long (depending on the parameter values). This is indeed an optimal strategy in this case, as we now illustrate.

First, however, we need to figure out, if this strategy is adopted, when the ideal time to turn on maximum reproduction is. To do so, we will assume that

$$\gamma(t) = \kappa\bar{H}(t - d_P),$$

where $\bar{H}(x)$ is the Heaviside function with $\bar{H}(0) = 1$, and $d_P = T - \bar{d_P}$, where $\bar{d_P}$ is to be determined. Plugging this $\gamma(t)$ into (3.1) and assuming $0 \leq d_P \leq T$ and $r \neq \kappa$, we obtain the following:

$$
\begin{aligned}
&W_0\left(a\cdot\exp(rT-\kappa(T-d_P))+b\kappa\int_{d_P}^{T}\exp(rt-\kappa(t-d_P))dt\right)\\
&=W_0\left(a\cdot\exp(rT-\kappa(T-d_P))+\frac{b\kappa}{r-\kappa}\left(\exp(rT-\kappa(T-d_P))-\exp(rd_P)\right)\right).
\end{aligned}
$$

Next, we differentiate this with respect to d_P and set it equal to 0 to solve for the value of d_P which maximizes this function:

$$
W_0\left(a\kappa\cdot\exp(rT-\kappa(T-d_P))+\frac{b\kappa}{r-\kappa}(\kappa\cdot\exp(rT-\kappa(T-d_P))-r\cdot\exp(rd_P))\right)=0.
$$

Now, solving this for d_P, we find that

$$
\begin{aligned}
\kappa\left(a+\frac{b\kappa}{r-\kappa}\right)\exp(rT-\kappa(T-d_P)) &= \frac{br\kappa}{r-\kappa}\exp(rd_P)\\
\frac{a(r-\kappa)+b\kappa}{r-\kappa} &= \frac{br}{r-\kappa}\exp((T-d_P)(\kappa-r))\\
\ln\left(\frac{a(r-\kappa)+b\kappa}{br}\right) &= (T-d_P)(\kappa-r)\\
T-\frac{1}{r-\kappa}\ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right) &= d_P.
\end{aligned}
$$

If $r=\kappa$, then, just like the annuals case, the given expression for d_P is undefined, meaning that a different expression for the starting time for reproduction is needed; we'll call this d_P^*. So, plugging in $\gamma(t)=\kappa\bar{H}(t-d_P^*)$, where $0\le d_P^*\le T$, into (3.1) obtains

$$
\begin{aligned}
&W_0\left(a\cdot\exp(\kappa T-\kappa(T-d_P^*))+b\kappa\int_{d_P^*}^{T}\exp(\kappa t-\kappa(t-d_P^*))dt\right)\\
&=W_0\left(a\cdot\exp(\kappa d_P^*)+b\kappa(T-d_P^*)\exp(\kappa d_P^*)\right).
\end{aligned}
$$

Differentiating this with respect to d_P^* and setting it equal to 0, we can solve for the d_P^* which maximizes (3.1) as follows:

$$\begin{aligned}
W_0\left(a\kappa \cdot \exp(kd_P^*) + b\kappa^2 \cdot \exp(kd_P^*)(T - d_P^*) - b\kappa \cdot \exp(kd_P^*)\right) &= 0 \\
1 + (b/a)\kappa(T - d_P^*) - b/a &= 0 \\
1 + (b/a)(T\kappa - 1) &= (b/a)\kappa d_P^* \\
d_P^* &= T - \frac{1}{\kappa} + \frac{1}{(b/a)\kappa} \\
&= T - \frac{b/a - 1}{(b/a)\kappa}.
\end{aligned}$$

As in the annuals case, to verify that these times do indeed maximize the objective function when assuming $\gamma(t) = \kappa\bar{H}(t - d)$, one can use the Second Derivative Test.

Remark: One could also obtain d_P^* by simply computing $\lim_{r\to\kappa} d_P$. Further, once d_P and d_P^* are known, d_A and d_A^* can be obtained by simply computing $\lim_{a\to 0^+} d_P$ and $\lim_{a\to 0^+} d_P^*$, respectively.

So, choosing

$$\begin{aligned}
d_P &= T - \frac{1}{r - \kappa}\ln\left(\frac{(b/a)r}{r - \kappa + (b/a)\kappa}\right) \\
d_P^* &= T - \frac{b/a - 1}{(b/a)\kappa},
\end{aligned}$$

we return to Theorems 3.1 and 3.2. As in the annuals case, should the given formulas above result in $d_P < 0$ (or $d_P^* < 0$), then we will simply choose $d_P = 0$, meaning that the plants will reproduce all season long; this is justified mathematically in the proof of Theorem 3.5. Unlike in the annuals case, it is possible that the expression for d_P is greater than T; however, we will show that the only way this occurs is when the conditions in Lemma 3.4 are met.

With all of this in mind, we have the following theorem:

Theorem 3.5: If $a > 0$, then $\gamma(t) = \kappa\bar{H}(t - d_P)$ is an optimal control for (3.1-3.3), replacing d_P with d_P^* if $r = \kappa$.

Proof: We begin with the case $r \neq \kappa$. So, plugging in $\gamma(t) = \kappa\bar{H}(t - d_P)$ into (3.11) gives us

$$p(t) = \begin{cases} a \cdot \exp\left(r(T-t) - \kappa(T-d_P)\right) & \\ \quad +b\kappa \int_{d_P}^{T} \exp\left(r(s-t) - \kappa(s-d_P)\right) ds & t < d_P \\ a \cdot \exp\left(r(T-t) - \kappa(T-t)\right) & \\ \quad +b\kappa \int_{t}^{T} \exp\left(r(s-t) - \kappa(s-t)\right) ds & t \geq d_P \end{cases}$$

$$= \begin{cases} \left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(r(T-t) - \kappa(T-d_P)\right) - \frac{b\kappa}{r-\kappa} \exp(r(d_P - t)) & t < d_P \\ \left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(r(T-t) - \kappa(T-t)\right) - \frac{b\kappa}{r-\kappa} & t \geq d_P \end{cases}.$$

For this $\gamma(t)$,

$$W_t = \begin{cases} W_0 \cdot \exp(rt) & t < d_P \\ W_0 \cdot \exp(rt - \kappa(t - d_P)) & t \geq d_P \end{cases},$$

so we then find the Hamiltonian for this $\gamma(t)$ as follows:

$$\begin{aligned}
H(t, W_t, \gamma(t), p(t)) &= W_t \cdot (rp(t) + \gamma(t)(b - p(t))) \\
&= \begin{cases} W_t \cdot (rp(t)) & t < d_P \\ W_t \cdot (rp(t) + \kappa(b - p(t))) & t \geq d_P \end{cases} \\
&= \begin{cases} rW_0 \left(\left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(rT - \kappa(T - d_P)\right) \right. \\ \qquad \left. -\frac{b\kappa}{r-\kappa} \exp(rd_P)\right) & t < d_P \\ rW_0 \left(\left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(rT - \kappa(T - d_P)\right) \right. \\ \qquad \left. -\frac{b\kappa}{r-\kappa} \exp(rt - \kappa(t - d_P))\right) \\ +W_0\kappa \left(b \cdot \exp(rt - \kappa(t - d_P)) \right. \\ \qquad - \left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(rT - \kappa(T - d_P)\right) \\ \qquad \left. +\frac{b\kappa}{r-\kappa} \exp(rt - \kappa(t - d_P))\right) & t \geq d_P \end{cases}
\end{aligned}$$

$$H(t, W_t, v, p(t)) = \begin{cases} rW_0 \left(\left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(rT - \kappa(T - d_P)\right) \right. \\ \qquad \left. -\frac{b\kappa}{r-\kappa} \exp(rd_P)\right) \\ +W_0 v \left(b \cdot \exp(rt) + \frac{b\kappa}{r-\kappa} \exp(rd_P) \right. \\ \qquad \left. - \left(a + \frac{b\kappa}{r-\kappa}\right) \exp(rT - \kappa(T - d_P))\right) & t < d_P \\ rW_0 \left(\left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(rT - \kappa(T - d_P)\right) \right. \\ \qquad \left. -\frac{b\kappa}{r-\kappa} \exp(rt - \kappa(t - d_P))\right) \\ +W_0 v \left(b \cdot \exp(rt - \kappa(t - d_P)) \right. \\ \qquad - \left(a + \frac{b\kappa}{r-\kappa}\right) \exp\left(rT - \kappa(T - d_P)\right) \\ \qquad \left. +\frac{b\kappa}{r-\kappa} \exp(rt - \kappa(t - d_P))\right) & t \geq d_P \end{cases}.$$

We now need to check that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

To do this, we begin with the branch where $t < d_P$. Here, we note that only one term of $H(t, W_t, v, p(t))$ is dependent on v; namely,

$$W_0 v \left(b \cdot \exp(rt) + \frac{b\kappa}{r-\kappa} \exp(rd_P) - \left(a + \frac{b\kappa}{r-\kappa} \right) \exp(rT - \kappa(T - d_P)) \right).$$

We want to show that this is maximized when $v = 0$, or, equivalently,

$$W_0 \left(b \cdot \exp(rt) + \frac{b\kappa}{r-\kappa} \exp(rd_P) - \left(a + \frac{b\kappa}{r-\kappa} \right) \exp(rT - \kappa(T - d_P)) \right) \leq 0 \tag{3.12}$$

for all $t < d_P$. But, we note that the left side of (3.12) clearly strictly increases with respect to t since $W_0, b > 0$, and so it will suffice to show it holds when $t = d_P$. We also note that, if $d_P = 0$, then this branch is irrelevant, and so we can take $d_P = T - \frac{1}{r-\kappa} \ln \left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa} \right)$. So, we plug this value in for t and note that:

$$\begin{aligned}
W_0 \left(b \cdot \exp(rd_P) - \left(a + \frac{b\kappa}{r-\kappa} \right) \exp(rT - \kappa(T - d_P)) + \frac{b\kappa}{r-\kappa} \exp(rd_P) \right) &\leq 0 \\
1 - \left(\frac{a}{b} + \frac{\kappa}{r-\kappa} \right) (\exp((r-\kappa)(T - d_P))) - \frac{\kappa}{r-\kappa} &\leq 0 \\
1 - \frac{a(r-\kappa) + b\kappa}{b(r-\kappa)} \left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa} \right) - \frac{\kappa}{r-\kappa} &\leq 0 \\
1 - \frac{r}{r-\kappa} - \frac{\kappa}{r-\kappa} &\leq 0 \\
0 &\leq 0.
\end{aligned}$$

Thus, (3.12) holds.

We next look at the branch where $t \geq d_P$. As before, only one term of $H(t, W_t, v, p(t))$ is dependent on v; namely,

$$W_0 v \cdot \exp(rt - \kappa(t - d_P)) \left(b - \left(a + \frac{b\kappa}{r - \kappa}\right) \cdot \exp\left(r(T - t) - \kappa(T - t)\right) + \frac{b\kappa}{r - \kappa}\right).$$

We want to show that this is maximized when $v = \kappa$, or, equivalently,

$$W_0 \left(\left(b + \frac{b\kappa}{r - \kappa}\right) \exp(rt - \kappa(t - d_P)) - \left(a + \frac{b\kappa}{r - \kappa}\right) \exp(rT - \kappa(T - d_P))\right) \geq 0. \tag{3.13}$$

Note that the partial derivative with respect to t of the left side of (3.13) is

$$W_0 br \cdot \exp(rt - \kappa(t - d_P)),$$

which is positive for all $t \geq d_P$, and hence the left side of this inequality is strictly increasing, meaning it will again suffice to prove the inequality is true when $t = d_P$. Plugging this in yields

$$W_0 \left(\left(b + \frac{b\kappa}{r - \kappa}\right) \exp(r d_P) - \left(a + \frac{b\kappa}{r - \kappa}\right) \exp(rT - \kappa(T - d_P))\right) \geq 0.$$

The left side of this inequality is equal to 0 when $d_P = T - \frac{1}{r-\kappa} \ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right)$, as shown previously, and hence (3.13) holds. Should this expression be negative, then, by the fact that the left side of (3.13) is strictly increasing, the above inequality would still hold. Thus, we have shown

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)),$$

and hence the necessary condition (Theorem 3.1) holds.

Finally, we need to check that the sufficient condition (Theorem 3.2) holds. So, let $\bar{\gamma}(t) \in M$ be some other control with $\bar{W}_t$ the corresponding constraint solution. Then,

$$\begin{aligned} &H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \\ &= (\bar{W}_t - W_t) \cdot (rp(t)) + (\bar{W}_t \cdot \bar{\gamma}(t) - W_t \cdot \gamma(t))(b - p(t)) \end{aligned}$$

and

$$\frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t)) \cdot (\bar{W}_t - W_t) = (\bar{W}_t - W_t) \cdot (rp(t) + \gamma(t)(b - p(t))).$$

So, for Theorem 3.2 to hold, we need to show that

$$\bar{\gamma}(t)(b - p(t)) \leq \gamma(t)(b - p(t))$$

By the work done previously, we know that $b - p(t) < 0$ if $t < d_P$ and $b - p(t) \geq 0$ if $t \geq d_P$. So, the above inequality reduces to

$$\begin{cases} \bar{\gamma}(t) \geq 0 & t < d_P \\ \bar{\gamma}(t) \leq \kappa & t \geq d_P \end{cases}.$$

This is clearly true by definition of M, and hence, for any $\bar{\gamma}(t) \in M$,

$$H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t))$$

for all $t \in [0, T]$. Thus, by Theorem 3.2, $\gamma(t) = \kappa \bar{H}(t - d_P)$ is an optimal control when $r \neq \kappa$. Should the expression for d_P be negative (hence, we'd take $d_P = 0$), then, as indicated in the proof, $\gamma(t) = \kappa$ is an optimal control.

Next, we assume that $r = \kappa$ and proceed in the same way. So, we first plug in $\gamma(t) = \kappa \bar{H}(t - d_P^*)$ into the formula for $p(t)$ and obtain:

$$p(t) = \begin{cases} a \cdot \exp\left(\kappa(T-t) - \kappa(T - d_P^*)\right) & \\ +b\kappa \int_{d_P^*}^{T} \exp\left(\kappa(s-t) - \kappa(s - d_P^*)\right) ds & t < d_P^* \\ a \cdot \exp\left(\kappa(T-t) - \kappa(T-t)\right) & \\ +b\kappa \int_{t}^{T} \exp\left(\kappa(s-t) - \kappa(s-t)\right) ds & t \geq d_P^* \end{cases}$$

$$= \begin{cases} (a + b\kappa(T - d_P^*)) \exp(\kappa(d_P^* - t)) & t < d_P^* \\ a + b\kappa(T-t) & t \geq d_P^* \end{cases}.$$

For this $\gamma(t)$,

$$W_t = \begin{cases} W_0 \cdot \exp(\kappa t) & t < d_P^* \\ W_0 \cdot \exp(\kappa d_P^*) & t \geq d_P^* \end{cases},$$

and hence we find the Hamiltonian for this $\gamma(t)$ as follows:

$$\begin{aligned}
H(t, W_t, \gamma(t), p(t)) &= W_t \cdot (\kappa p(t) + \gamma(t)(b - p(t))) \\
&= \begin{cases} W_t \cdot (\kappa p(t)) & t < d_P^* \\ W_t \cdot (\kappa b) & t \geq d_P^* \end{cases} \\
&= \begin{cases} W_0 \kappa (a + b\kappa(T - d_P^*)) \exp(\kappa d_P^*) & t < d_P^* \\ W_0 b\kappa \cdot \exp(\kappa d_P^*) & t \geq d_P^* \end{cases} \\
H(t, W_t, v, p(t)) &= \begin{cases} W_0 \left(\kappa(a + b\kappa(T - d_P^*)) \exp(\kappa d_P^*)\right. & \\ \qquad \left. + v\left(b \cdot \exp(\kappa t) - (a + b\kappa(T - d_P^*)) \exp(\kappa d_P^*)\right)\right) & t < d_P^* \\ W_0 \cdot \exp(\kappa d_P^*) & \\ \cdot \left(\kappa(a + b\kappa(T - t)) + v(b - a - b\kappa(T - t))\right) & t \geq d_P^* \end{cases}.
\end{aligned}$$

We now need to check that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)).$$

Assuming $t < d_P^*$, we note that the only term of $H(t, W_t, v, p(t))$ that depends on v is

$$W_0 v \left(b \cdot \exp(\kappa t) - (a + b\kappa(T - d_P^*)) \exp(\kappa d_P^*)\right).$$

Note that this branch is only relevant when $d_P^* > 0$. Hence, we take $d_P^* = T - \frac{b/a - 1}{(b/a)\kappa}$, and plugging this in above yields

$$W_0 b v \left(\exp(\kappa t) - \exp(\kappa d_P^*)\right).$$

Since e^x is a strictly increasing function, this is clearly negative for all $t < d_P^*$, meaning that, to maximize it with respect to $v \in [0, \kappa]$, we need to set $v = 0$.

Next, assuming $t \geq d_A^*$, we note that the only term of $H(t, W_t, v, p(t))$ that depends on v is

$$W_0 v \cdot \exp(\kappa d_P^*)(b - a - b\kappa(T - t)).$$

Determining what value of v will maximize this comes down to determining the sign of

$$b - a - b\kappa(T - t) = b(1 + \kappa t - \kappa T) - a.$$

Note that, at $t = T - \frac{b/a-1}{(b/a)\kappa}$, the above is equal to 0. Further, since this quantity clearly increases with respect to t, then it is nonnegative for all $t \geq d_P^*$. Hence, to maximize $H(t, W_t, v, p(t))$ with respect to v when $t \geq d_A^*$, we need to set $v = \kappa$. This, along with the above, proves that

$$H(t, W_t, \gamma(t), p(t)) = \max_{v \in [0,\kappa]} H(t, W_t, v, p(t)),$$

and hence the necessary condition (Theorem 3.1) holds.

Now, for sufficiency, we need to verify Theorem 3.2 holds. So, let $\bar{\gamma}(t) \in M$ be some other control with $\bar{W}_t$ the corresponding constraint solution. Then,

$$\begin{aligned} &H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \\ &= (\bar{W}_t - W_t) \cdot (rp(t)) + (\bar{W}_t \cdot \bar{\gamma}(t) - W_t \cdot \gamma(t))(b - p(t)) \end{aligned}$$

and

$$\frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t)) \cdot (\bar{W}_t - W_t) = (\bar{W}_t - W_t) \cdot (\kappa p(t) + \gamma(t)(b - p(t))).$$

So, for Theorem 3.2 to hold, we need to show that

$$\bar{\gamma}(t)(b-p(t)) \leq \gamma(t)(b-p(t)).$$

By the work to verify that Theorem 3.1 holds, we notice that $b-p(t)<0$ if $t<d_P^*$ and $b-p(t)\geq 0$ if $t\geq d_P^*$. With this in mind, this inequality reduces to

$$\begin{cases} \bar{\gamma}(t) \geq 0 & t < d_P^* \\ \bar{\gamma}(t) \leq \kappa & t \geq d_P^* \end{cases}$$

This is clearly true by definition of M, and hence, for any $\bar{\gamma}(t) \in M$,

$$H(t, \bar{W}_t, \bar{\gamma}(t), p(t)) - H(t, W_t, \gamma(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t, \gamma(t), p(t))$$

for all $t \in [0,T]$. Thus, by Theorem 3.2, $\gamma(t) = \kappa \bar{H}(t-d_P^*)$ is an optimal control when $r \neq \kappa$. Should the expression for d_P be negative (hence, we'd take $d_P^*=0$), then, as indicated in the proof, $\gamma(t)=\kappa$ is an optimal control.

This completes the proof of Theorem 3.5.

Remark 1: In the same way as we did in Remark 1 of Theorem 3.3, we can show that, except for the point $t = d_P$ (or d_P^*) if $d_P > 0$, then the optimal strategy $\gamma^*(t) = \kappa \bar{H}(t-d_P)$ is uniquely determined. This is because $a<b$ and $p(t)$ is strictly monotone decreasing if $\gamma(t)>0$.

Remark 2: We also want to know what the corresponding optimal value for the objective function is. Since Theorem 3.5 gives us an optimal control when $a>0$, then we can simply plug it in to (3.1) to find the corresponding value.

So, plugging in $\gamma^*(t) = \kappa\bar{H}(t - d_P)$ (use d_P^* if $r = \kappa$) gives an optimal value of

$$\begin{aligned}
&aW_T + b\int_0^T \gamma^*(t)W_t dt \\
&= aW_0 \cdot \exp(rT - \kappa(T - d_P)) + b\kappa W_0 \int_{d_P}^T \exp(rt - \kappa(t - d_P))dt \\
&= W_0 \left(\left(a + \frac{b\kappa}{r - \kappa} \right) \exp(rT - \kappa(T - d_P)) - \frac{b\kappa}{r - \kappa} \exp(rd_P) \right)
\end{aligned}$$

if $r \neq \kappa$, and

$$\begin{aligned}
aW_T + b\int_0^T \gamma^*(t)W_t dt &= aW_0 \cdot \exp(\kappa d_P^*) + b\kappa W_0 \int_{d_P^*}^T \exp(\kappa d_P^*)dt \\
&= W_0 \cdot \exp(\kappa d_P^*) \left(a + b\kappa(T - d_P^*) \right)
\end{aligned}$$

if $r = \kappa$.

Remark 2: Unlike the annuals case, in the perennials case, it is possible for $d_P \geq T$ (or $d_P^* \geq T$) depending on the parameter values. Specifically, if $d_P \geq T$, meaning that the population never reproduces during the season, and d_P is defined (that is, if $r < \kappa$, $b/a > 1 - \frac{r}{\kappa}$), then it is necessary that $b/a \leq 1$, essentially a converse of Lemma 3.4. To see why, we simply note that, for $d_P \geq T$, then we need:

$$\frac{1}{r - \kappa} \ln\left(\frac{(b/a)r}{r - \kappa + (b/a)\kappa} \right) \leq 0.$$

If $r < \kappa$, requiring $b/a > 1 - \frac{r}{\kappa}$, then we need:

$$\begin{aligned} \ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right) &\geq 0 \\ \frac{(b/a)r}{r-\kappa+(b/a)\kappa} &\geq 1 \\ (b/a)(r-\kappa) &\geq r-\kappa \\ b/a &\leq 1. \end{aligned}$$

If $r > \kappa$, then, except for switching "$\geq$" to "$\leq$" in the appropriate places above, the exact same argument holds. Note that, if $r < \kappa$, the only way that d_P can't be defined is if $b/a \leq 1$ anyway, which means Lemma 3.4 holds.

Also, if we look at $d_P^* = T - \frac{b/a-1}{(b/a)\kappa}$, we see that, for $d_P^* \geq T$, then, clearly, we need $b/a \leq 1$, again serving as essentially a converse for Lemma 3.4. In summary, if $b/a > 1$, then the plants will reproduce, beginning at some point during the season (possibly at the beginning) and lasting until the end of the season.

So, according to Theorem 3.5, whenever $b/a > 1$, this optimal strategy is, as in the annuals case, to either initially not reproduce and then, at a designated time in the future, pour all available resources into reproduction, or to reproduce all season long. We will investigate under what condition(s) season-long reproduction is the optimal strategy in the next section.

3.4 When is Season-Long Reproduction Optimal?

Our next task is to investigate under what condition(s) the plant populations should reproduce all season long for maximal yields next season; that is, what conditions on the parameters ensure that d_A or d_P (d_A^* or d_P^* if $r = \kappa$) will be 0? In order to get

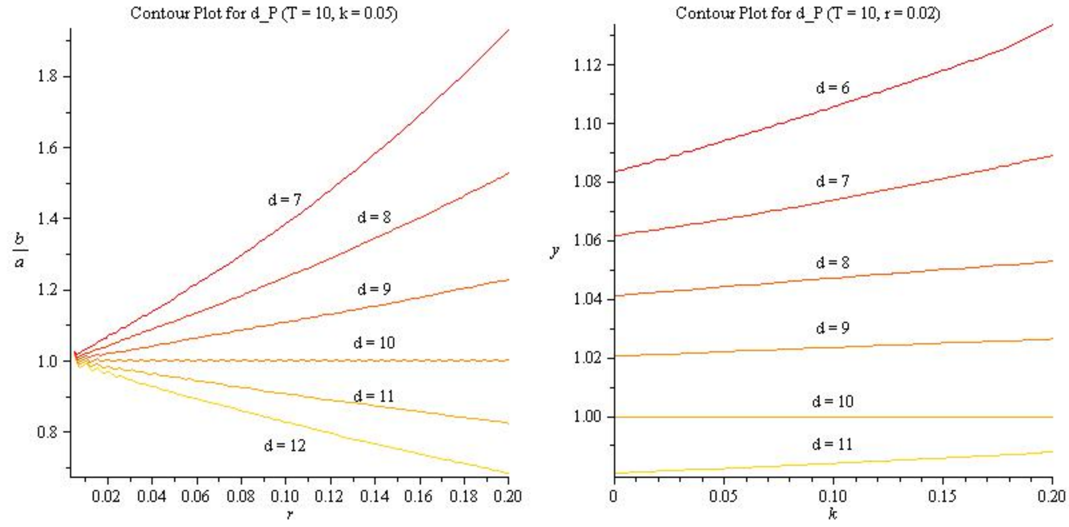

Figure 3.1: Contour plots of d_P

an idea of what roles the parameters play in affecting the value of the starting time, we look at two contour plots for d_P, created using Maple, which compare the ratio b/a to r and κ (one is fixed, the other varies for each plot) to get an idea for how the different parameters affect the value of d_P. Figure 3.1 shows the contour plots with $T = 10$ and values of d_P chosen relatively close to T, with $\kappa = 0.05$ in the first plot and $r = 0.02$ in the second (choosing them to be any arbitrary positive value doesn't affect the overall shape of the contour plot).

We note a few facts from these graphs. First, the contours where $d_P \geq T$ each stay below the line $b/a = 1$, which is consistent with Lemma 3.4, and the contours where $d_P < T$ each stay above the line $b/a = 1$, which is consistent with Theorem 3.5. Secondly, the contours $d = 7$, $d = 8$, and $d = 9$ each increase (with respect to b/a) when r or κ is increased. That is, if r or κ increases while b/a remains fixed, the time that reproduction should start becomes later in the season, and, if b/a increases while r, κ remain fixed, the time that reproduction should start becomes earlier in the season. Both of these observations make biological sense because, if

r is increasing, holding κ and b/a fixed, the population can grow faster in a given instant, meaning there is incentive for it to wait in order to begin reproduction since it will have more biomass to work with. Likewise, if κ is increasing, holding r and b/a fixed, the population can invest more of its total biomass into reproduction at any given instant, meaning it can afford to wait longer, and hence spend more time growing, before it needs to reproduce. If we assume that b/a is increasing, this implies that either b is increasing and/or a is decreasing. So, the population has a higher reproductive utility and/or has a lower proportion of adult biomass surviving from the end of one season to the start of the next, respectively, meaning there is incentive for the population to begin reproduction earlier in the season.

Finally, note that there are holes in these contours where $r = \kappa$; however, these are not visible on the plots. In this case, however, we can quickly look at the expression for d_P^* and, omitting the reference to r in the previous paragraph, we note that all of the observations still hold (since $0 < \kappa < 1$, as b/a increases, then d_P^* decreases).

Remark: It should also be noted that drawing a contour plot for d_A, comparing r and κ, leads to the same conclusions as above (ignoring the references to a and b).

Although this plot gives us an idea as to the types of conditions that guarantee season-long reproduction is optimal, we want to be more precise, both quantitatively and qualitatively, about when this is the case. We'll begin by looking at annuals. Assuming that $r \neq \kappa$, and recalling that $d_A = T - \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right)$ whenever the expression on the right is nonnegative, if we want $d_A = 0$, then we need:

$$T\kappa \leq \frac{1}{r/\kappa - 1} \ln\left(\frac{r}{\kappa}\right). \tag{3.14}$$

To see when this can occur, we consider the right side and note the following properties of the function

$$f(x) = \frac{\ln x}{x-1},\ x \in (0, \infty),\ x \neq 1.$$

First, we see that

$$f'(x) = \frac{\frac{x-1}{x} - \ln x}{(x-1)^2}.$$

Note that, since $\frac{d}{dx}\left(\frac{x-1}{x}\right) = \frac{1}{x^2}$ and $\frac{d}{dx}(\ln x) = \frac{1}{x}$, then, clearly, both of these functions are increasing on $(0, \infty)$, but, since $\ln x$ increases faster when $x > 1$, and $\frac{x-1}{x} = \ln x = 0$ at $x = 1$, then it follows that $f(x)$ is decreasing on $(1, \infty)$. Likewise, $\frac{x-1}{x}$ increases faster when $0 < x < 1$, but, since $\frac{x-1}{x} = \ln x = 0$ at $x = 1$, then it follows that $f(x)$ is also decreasing on $(0, 1)$. Hence, $f(x)$ is strictly decreasing on its domain. We also note that

$$\lim_{x\to 1} \frac{\ln x}{x-1} = 1$$
$$\lim_{x\to \infty} \frac{\ln x}{x-1} = 0$$
$$\lim_{x\to 0^+} \frac{\ln x}{x-1} = \infty,$$

where the first two limits were computed using l'Hospital's Rule (see, for example, [25, p. 299]). So, we see that, for (3.14) to hold, we require $T\kappa < 1$ if $r > \kappa$ (if $r < \kappa$, then it is permissible for $T\kappa \geq 1$).

However, this is only a necessary condition; a sufficient condition comes from solving the equation

$$\frac{\ln x}{x-1} = T\kappa.$$

Calling LamW(x) the Lambert W function (that is, the function satisfying $x =$

$\operatorname{LamW}(x) \cdot \exp(\operatorname{LamW}(x)))$, we note that we can solve this as follows:

$$\begin{aligned}
\ln x &= (x-1)T\kappa \\
x &= \exp(T\kappa x - T\kappa) \\
-T\kappa x \cdot \exp(-T\kappa x) &= -T\kappa \cdot \exp(-T\kappa) \\
-T\kappa x &= \operatorname{LamW}(-T\kappa \cdot \exp(-T\kappa)) \\
x &= -\frac{1}{T\kappa}\operatorname{LamW}(-T\kappa \cdot \exp(-T\kappa)).
\end{aligned}$$

Plugging in $\frac{r}{\kappa}$ for x yields:

$$\frac{r}{\kappa} = -\frac{1}{T\kappa}\operatorname{LamW}(-T\kappa \cdot \exp(-T\kappa)).$$

Because the argument for the Lambert W function is contained in the interval $\left[-\frac{1}{e}, 0\right)$ (the function $h(x) = xe^x$ has minimum value $-\frac{1}{e}$ at $x = -1$ and is negative on $(-\infty, 0)$), then there are actually two possible real-valued solutions to the equation ([6, pp. 330-331]):

$$\frac{r}{\kappa} = -\frac{1}{T\kappa}\operatorname{LamW}_0(-T\kappa \cdot \exp(-T\kappa))$$

OR

$$\frac{r}{\kappa} = -\frac{1}{T\kappa}\operatorname{LamW}_{-1}(-T\kappa \cdot \exp(-T\kappa)),$$

where the subscripts on LamW refer to the branch number. To further interpret these two solutions, we turn to [6, pp. 330-331, 341-345] for more information (the reader who is interested in proofs of the following results may refer to these pages).

The 0 branch is known as the principal branch; it is the unique real-valued branch of the Lambert W function whenever the argument is positive, but is real-valued as long as its argument is at least $-\frac{1}{e}$. The only other branch which can be real-valued is the -1 branch; it, however, is only real-valued when its argument is in the interval $\left[-\frac{1}{e}, 0\right)$. The two branches coincide when the argument is $-\frac{1}{e}$, or when $T\kappa = 1$ (in this case, both return a value of -1); otherwise, the two branches produce different results (both will be negative, however). Specifically, the principal branch will return values at least -1, but the -1 branch will return values only up to -1.

Keeping this in mind, we note that, if $T\kappa < 1$, it would then follow that, by definition of LamW,

$$\mathrm{LamW}_0(-T\kappa \cdot \exp(-T\kappa)) = -T\kappa.$$

This would then imply that $r = \kappa$, which we assumed was not true. But, the -1 branch would return a value which would be less than -1, so, if $T\kappa < 1$, we need to use the -1 branch for a solution which actually exists. On the other hand, if $T\kappa \geq 1$, then

$$\mathrm{LamW}_{-1}(-T\kappa \cdot \exp(-T\kappa)) = -T\kappa.$$

So, it follows that, if $T\kappa > 1$, we need to use the principal branch for a solution that actually exists since it will have value greater than -1.

So, keeping the properties of $f(x)$ in mind, (3.14) is satisfied if

$$\frac{r}{\kappa} \leq -\frac{1}{T\kappa}\mathrm{LamW}(-T\kappa \cdot \exp(-T\kappa)),$$

where the branch number of LamW is 0 if $T\kappa < 1$ or -1 if $T\kappa > 1$. So, in summary, $d_A = 0$ if

$$\frac{r}{\kappa} \leq -\frac{1}{T\kappa}\mathrm{LamW}(-T\kappa \cdot \exp(-T\kappa)),$$

assuming $T\kappa \neq 1$. If $T\kappa = 1$, then, to have $d_A = 0$, we would need

$$1 \leq \frac{1}{rT - 1}\ln(rT).$$

But, by the discussion of $f(x)$, this will be true so long as $rT < 1$, or, put another way, $r < \kappa$.

Although this gives a mathematical condition for when season-long reproduction is optimal, it is also important to see what biological conditions will allow this to occur. Clearly, looking at the expression for d_A, one way to ensure season-long reproduction is optimal is to have a sufficiently short season (T is sufficiently small), as this will eventually make $d_A = 0$. This makes sense because a short season means the plants won't have a lot of time to invest in growth; if they do, they may not have enough time to sufficiently reproduce for next season.

Let's now look at what happens when we change either r or κ in the expression for d_A, keeping the other parameters fixed:

$$\begin{aligned}
\frac{\partial}{\partial r}\left(T - \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right) &= \frac{1}{(r-\kappa)^2}\ln\left(\frac{r}{\kappa}\right) - \frac{1}{r-\kappa}\cdot\frac{\kappa}{r}\cdot\frac{1}{\kappa} \\
&= \frac{1}{(r-\kappa)^2}\ln\left(\frac{r}{\kappa}\right) - \frac{1}{r(r-\kappa)} \\
\frac{\partial}{\partial \kappa}\left(T - \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right) &= -\frac{1}{(r-\kappa)^2}\ln\left(\frac{r}{\kappa}\right) + \frac{1}{r-\kappa}\cdot\frac{\kappa}{r}\cdot\frac{r}{\kappa^2} \\
&= -\frac{1}{(r-\kappa)^2}\ln\left(\frac{r}{\kappa}\right) + \frac{1}{\kappa(r-\kappa)}.
\end{aligned}$$

If we want these partial derivatives to be positive, we need:

$$\begin{aligned}
\frac{r-\kappa}{r} &> \ln\left(\frac{r}{\kappa}\right) \\
1 - \frac{\kappa}{r} &> -\ln\left(\frac{\kappa}{r}\right) \\
\ln\left(\frac{\kappa}{r}\right) &< \frac{\kappa}{r} - 1
\end{aligned}$$

and

$$\begin{aligned}\ln\left(\frac{r}{\kappa}\right) &< \frac{r-\kappa}{\kappa}\\ \ln\left(\frac{r}{\kappa}\right) &< \frac{r}{\kappa}-1.\end{aligned}$$

So, in either case, we are investigating an inequality of the form $\ln x < x-1$ for any $x > 0, x \neq 1$. As it turns out, this is always true. To see why, we first note that $\ln x = x - 1 = 0$ at $x = 1$, and, since $\frac{d}{dx}\ln x = \frac{1}{x}$ for all $x > 0$, it clearly increases at a slower rate than $x-1$ for $x > 1$. Likewise, going backwards from $x = 1$, $\ln x$ decreases faster than $x - 1$. As a result, $\ln x < x - 1$ for all $x > 0, x \neq 1$. Hence, as either r or κ increase, d_A increases.

Thus, if we want $d_A = 0$, we could have r and/or κ sufficiently small. The former says that the plants' growth rate is small, meaning that waiting a while before reproducing won't result in having significantly more biomass to play with than if they started reproducing early. So, spending more time growing would then mean the plants may not have enough time to guarantee a high yield for next season, as more time spent growing means less time is spent reproducing. The latter says that the maximum reproduction rate at any time t is small, meaning that, since the plants can't invest much of their available biomass at any one time into reproduction, waiting to reproduce won't give the plants enough time to ensure a high yield for next season. In fact, it is not difficult to see that

$$\lim_{r\to 0^+} T - \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right) = \lim_{\kappa\to 0^+} T - \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right) = -\infty.$$

This confirms, mathematically, that $d_A = 0$ if either r and/or κ is sufficiently small.

Next, if $r = \kappa$, recalling that $d_A^* = T - \frac{1}{\kappa}$ as long as the right hand side is nonnegative, then, clearly, $d_A^* = 0$ if $T\kappa \leq 1$. This says that, if the season is sufficiently short, and/or the maximum reproduction rate at any time t is sufficiently small, it is optimal for the plants to reproduce all season long. The biological explanations for these are the same as for d_A.

We next consider the perennials case with reproduction (that is, $b/a > 1$), and we'll begin by looking at the case where $r \neq \kappa$. In this case, recall that the plants begin reproduction at time

$$d_P = T - \frac{1}{r-\kappa} \ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right)$$

if the expression on the right is positive. The optimal strategy of reproducing all season long occurs when the right-hand side of the expression is less than or equal to 0. So, for this to occur, first assuming $r > \kappa$, we note that we need

$$\begin{aligned} T - \frac{1}{r-\kappa} \ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right) &\leq 0 \\ T(r-\kappa) &\leq \ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right) \\ \exp(T(r-\kappa)) &\leq \frac{(b/a)r}{r-\kappa+(b/a)\kappa} \\ (r-\kappa)\cdot\exp(T(r-\kappa)) &\leq (b/a)\left(r-\kappa\cdot\exp(T(r-\kappa))\right). \end{aligned} \tag{3.15}$$

Likewise, if $r < \kappa$, then we need

$$(r-\kappa)\cdot\exp(T(r-\kappa)) \geq (b/a)\left(r-\kappa\cdot\exp(T(r-\kappa))\right). \tag{3.16}$$

We note that we have to check the sign of $r-\kappa\cdot\exp(T(r-\kappa))$ to see if (3.15) and (3.16) can be true or not; specifically, if $r > \kappa$, we need this quantity to be nonnegative, and, if $r < \kappa$, we need it to not be positive. So, for this quantity to be nonnegative, we need

$$\begin{aligned} r - \kappa \cdot \exp(T(r-\kappa)) &\geq 0 \\ \frac{r}{\kappa} &\geq \exp(T(r-\kappa)) \\ \ln\left(\frac{r}{\kappa}\right) &\geq T\kappa\left(\frac{r}{\kappa} - 1\right) \end{aligned}$$

$$\begin{cases} \frac{\ln(r/\kappa)}{(r/\kappa)-1} \geq T\kappa & r > \kappa \\ \frac{\ln(r/\kappa)}{(r/\kappa)-1} \leq T\kappa & r < \kappa \end{cases}. \tag{3.17}$$

Now, to determine when (or if) (3.15) and (3.16) can be true, we recall the properties of $f(x) = \frac{\ln x}{x-1}$ previously derived, and note that we require $T\kappa < 1$ if $r > \kappa$ or $T\kappa > 1$ if $r < \kappa$ since $f(x)$ is decreasing on $(0, 1)$ and $(1, \infty)$.

However, this is only a necessary condition; again, a sufficient condition comes from solving the equation

$$\frac{\ln x}{x-1} = T\kappa.$$

Taking $x = r/\kappa$, recall that the nontrivial, real solution of this equation is given by

$$\frac{r}{\kappa} = -\frac{1}{T\kappa}\mathrm{LamW}(-T\kappa \cdot \exp(-T\kappa)),$$

where the branch number of LamW is either 0 or -1, depending on whether $T\kappa > 1$ or $T\kappa < 1$, respectively.

So, going back to (3.15) and (3.16), if $r > \kappa$ and $T\kappa < 1$, then the value of r/κ given above is the breaking point for whether (3.17) is true or false. Thus, recalling the facts above, if r/κ is less than the above solution, then (3.17) is true; otherwise, it is false. Likewise, if $r < \kappa$ and $T\kappa > 1$, then, if r/κ is less than the above solution, (3.17) is false; otherwise, it is true.

Thus, tying this all together, we have proven the following lemma:

Lemma 3.6: If:

1. $\frac{r}{\kappa} < -\frac{1}{T\kappa}\text{LamW}(-T\kappa \cdot \exp(-T\kappa))$
2. $T\kappa < 1$ if $r > \kappa$ ($T\kappa \geq 1$ is permissible if $r < \kappa$),

then $d_P = 0$ if

$$b/a \geq \frac{(r-\kappa)\cdot\exp(T(r-\kappa))}{r-\kappa\cdot\exp(T(r-\kappa))}.$$

Remark: Should $\frac{r}{\kappa} = -\frac{1}{T\kappa}\text{LamW}(-T\kappa \cdot \exp(-T\kappa))$, or, put another way,

$$\frac{\ln(r/\kappa)}{(r/\kappa)-1} = T\kappa,$$

then we have that

$$r - \kappa\cdot\exp(T(r-\kappa)) = 0.$$

As a result, (3.15) and (3.16) reduce down to

$$\exp(T(r-\kappa)) \leq 0.$$

This is clearly false, and hence why we needed the strict inequality for r/κ in Lemma 3.6.

To see what biological conditions we need for $d_P = 0$, we proceed as in the annuals case and look at partial derivatives with respect to $y = b/a$, r, and κ. First, we remark that, as in the annuals case, if the season length, T, is sufficiently small, then this will certainly make $d_P = 0$.

The partial derivatives are:

$$\begin{aligned}
\frac{\partial}{\partial y}(d_P) &= -\frac{1}{r-\kappa}\cdot\frac{r-\kappa+y\kappa}{ry}\cdot\frac{r(r-\kappa+y\kappa)-ry\kappa}{(r-\kappa+y\kappa)^2} \\
&= -\frac{1}{y(r-\kappa+y\kappa)} \\
\frac{\partial}{\partial r}(d_P) &= \frac{1}{(r-\kappa)^2}\ln\left(\frac{ry}{r-\kappa+y\kappa}\right)-\frac{1}{r-\kappa}\cdot\frac{r-\kappa+y\kappa}{ry}\cdot\frac{y(r-\kappa+y\kappa)-ry}{(r-\kappa+y\kappa)^2} \\
&= \frac{1}{(r-\kappa)^2}\ln\left(\frac{ry}{r-\kappa+y\kappa}\right)-\frac{\kappa(y-1)}{r(r-\kappa)(r-\kappa+y\kappa)} \\
\frac{\partial}{\partial \kappa}(d_P) &= -\frac{1}{(r-\kappa)^2}\ln\left(\frac{ry}{r-\kappa+y\kappa}\right)-\frac{1}{r-\kappa}\cdot\frac{r-\kappa+y\kappa}{ry}\cdot\frac{ry(1-y)}{(r-\kappa+y\kappa)^2} \\
&= -\frac{1}{(r-\kappa)^2}\ln\left(\frac{ry}{r-\kappa+y\kappa}\right)+\frac{y-1}{(r-\kappa)(r-\kappa+y\kappa)}.
\end{aligned}$$

Since we are assuming that $y > 1$, then, clearly, $\frac{\partial}{\partial y}(d_P) < 0$, and so one condition to have season-long reproduction be optimal is to have b/a sufficiently large. This says that either the chances of reproductive biomass becoming full-grown adults is very high, the amount of times more biomass a full-grown adult has, on average, versus the reproductive investment to obtain that plant is very high, and/or the average survivorship of adult biomass from one season to the next is very small. All three of these make biological sense because having either reproductive survivorship or the growth factor be large means that an investment in reproduction will have a high yield for next season in terms of new biomass, and so it is definitely advantageous for the population to start reproduction early in this case. Also, having the survivorship of existing adults to next season be small means that, since very little existing biomass can be carried over to next season, it is best to invest as much as possible into seeds for next season to maximize next season's population. However, because $d_P \to d_A$ as $b/a \to \infty$, only adjusting b/a will not, in general, force $d_P = 0$ since it may still be that $d_A > 0$. Thus, r, κ, and/or T will likely need to be adjusted as well in order to force $d_P = 0$; this is also suggested by Lemma 3.6, since we require r/κ to be sufficiently small as a necessary condition for $d_P = 0$.

Next, we need to check the signs of the other two partial derivatives, and we'll begin with the one with respect to r. Specifically, if we want it to be positive, then we need

$$\begin{aligned}
\frac{1}{(r-\kappa)^2}\ln\left(\frac{ry}{r-\kappa+y\kappa}\right) &> \frac{\kappa(y-1)}{r(r-\kappa)(r-\kappa+y\kappa)}\\
\ln\left(\frac{ry}{r-\kappa+y\kappa}\right) &> \frac{\kappa(y-1)(r-\kappa)}{r(r-\kappa+y\kappa)}\\
&= \frac{\kappa(-r+\kappa-y\kappa+yr)}{r(r-\kappa+y\kappa)}\\
&= \frac{y\kappa}{r-\kappa+y\kappa}-\frac{\kappa}{r}\\
\ln\left(\frac{z}{m}\right) &> z-m,
\end{aligned}$$

where $z = \frac{y\kappa}{r-\kappa+y\kappa} > 0$ and $m = \frac{\kappa}{r} > 0$. So, essentially, we need to verify if $z/m > e^{z-m}$, or $ze^{-z} > me^{-m}$. First, let's check if $z > m$:

$$\begin{aligned}
\frac{y\kappa}{r-\kappa+y\kappa} &> \frac{\kappa}{r}\\
\frac{ry}{r-\kappa+y\kappa} &> 1\\
ry &> r-\kappa+y\kappa\\
y(r-\kappa) &> (r-\kappa)
\end{aligned}$$

So, $z > m$ if $r > \kappa$ and $z < m$ if $r < \kappa$. Note that, in the former case, this implies $m, z < 1$ and, in the latter, $m, z > 1$.

Looking at $g(x) = xe^{-x}$, we see that $g'(x) = (1-x)e^{-x}$, and hence $g(x)$ is increasing if $x < 1$ and is decreasing if $x > 1$. Tying all of this information together, we see that $ze^{-z} > me^{-m}$ as we wanted. So, this says that a condition for season-long reproduction to be optimal is if the growth rate is sufficiently small, the same as in the annuals case. In fact, we note that

$$\lim_{r\to 0^+} T - \frac{1}{r-\kappa}\ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right) = -\infty$$

So, a sufficiently small r is enough to guarantee that $d_P = 0$.

Finally, checking the sign of the partial derivative with respect to κ, if we want it to be positive, then we need

$$\begin{aligned}\frac{y-1}{(r-\kappa)(r-\kappa+y\kappa)} &> \frac{1}{(r-\kappa)^2}\ln\left(\frac{ry}{r-\kappa+y\kappa}\right)\\ \frac{(y-1)(r-\kappa)}{r-\kappa+y\kappa} &> \ln\left(\frac{ry}{r-\kappa+y\kappa}\right)\\ \frac{ry}{r-\kappa+y\kappa} - 1 &> \ln\left(\frac{ry}{r-\kappa+y\kappa}\right).\end{aligned}$$

So, essentially, we need to check that $x - 1 > \ln x$ for $x > 0, x \neq 1$ (we can rule $x = 1$ out because, here, that can only happen if $r = \kappa$ since $y > 1$). But, we've already proved that this is true when discussing the annuals case, and hence we see that another condition for season-long reproduction to be optimal is if the proportion of total biomass the plants can invest in reproduction is sufficiently small, just like in the annuals case. However, unlike the annuals case, we note that

$$\lim_{\kappa\to 0^+} T - \frac{1}{r-\kappa}\ln\left(\frac{(b/a)r}{r-\kappa+(b/a)\kappa}\right) = T - (1/r)\ln(b/a)$$

So, unless r is also sufficiently small and/or b/a is sufficiently large, then a very small κ does not guarantee that $d_P = 0$. This is due to perennials being able to carry some of their adult biomass over to next season, lessening the impact of a low value of κ.

Finally, we discuss the case where $r = \kappa$. Recall that, in this case, we found that

$$d_P^* = T - \frac{b/a - 1}{(b/a)\kappa}$$

is the optimal starting time for reproduction if $d_P^* > 0$. So, if we want $d_P^* = 0$, then we need

$$(b/a)(T\kappa - 1) \leq -1.$$

The only way for this to hold is if $T\kappa < 1$. If this is true, then, if

$$b/a \geq \frac{1}{1 - T\kappa},$$

we have that $d_P^* = 0$. Biologically, this says that, if the season is sufficiently short, or if only a small proportion of biomass is allowed to be invested in reproduction at a given instant, then, pending the return on invested adult biomass into reproduction, b/a, is sufficiently large (the smaller $T\kappa$ is, the larger b/a has to be for season-long reproduction to be optimal), it makes sense for the plants to reproduce all season long.

Remark: Since $d_P^* \to d_A^*$ as $b/a \to \infty$, it certainly makes sense to have, as b/a gets larger, the dominant condition for $d_P^* = 0$ to be $T\kappa < 1$, which was the condition needed for $d_A^* = 0$.

Chapter 4

The Stochastic Case

4.1 Solving for W_t

Recall that the optimization problem we are trying to solve is:

$$\text{Maximize} \quad E\left[aW_T + b\int_0^T \gamma(t)W_t dt\right] \tag{4.1}$$

$$\text{subject to} \quad dW_t = (r-\gamma(t))W_t dt + \sigma W_t dB_t \tag{4.2}$$

$$W_t \geq 0. \tag{4.3}$$

Compared to the deterministic case, the only extra term added to the constraint is $\sigma W_t dB_t$; this is the random, or "white noise," term. However, since $E[dB_t] = 0$ for any t, and the objective function involves taking the expected value of the same functional used in the deterministic case, it is logical to assume that an optimal control should be very close to, if not exactly the same, as the optimal control in the deterministic case. In fact, we will show that the controls we derived in the deterministic case are still optimal in this stochastic case.

The first step in proving this is to solve the stochastic differential equation (SDE) making up the first constraint. To do so, we need Ito's formula, given as Theorem 4.1.2 in Oksendal ([22, p. 44]):

Theorem 4.1 (1-D Ito's Formula): If X_t is a stochastic process which solves the SDE

$$dX_t = udt + vdB_t,$$

and $Y_t = f(t, X_t) \in C^{1,2}([0,\infty) \times \mathbb{R})$, then Y_t solves the SDE

$$dY_t = \left(\frac{\partial f}{\partial t} + \frac{1}{2} \frac{\partial^2 f}{\partial x^2} \right) dt + \frac{\partial f}{\partial x} dB_t.$$

Proof: A proof can be found in [22, pp. 46-48].

Remark: For our SDE, we are only concerned with having $X_t = B_t$; that is, $u = 0$ and $v = 1$.

However, because the optimal controls we found in the deterministic case may not be continuous, simply plugging in those choices for $\gamma(t)$ and applying Ito's formula to get a solution won't necessarily work. This is because the partial derivative of f with respect to t will not necessarily be continuous. Instead, we will apply Ito's formula on each interval where the controls are continuous, and then join those solutions together. Of course, we need to ensure that what we are doing results in a unique solution of the SDE; the following, which is Theorem 5.2.5 in Oksendal ([22, p. 66]), guarantees this:

Theorem 4.2: Suppose $c : [0,T] \times \mathbb{R} \to \mathbb{R}$ and $\sigma : [0,T] \times \mathbb{R} \to R$ are measurable functions which satisfy the following for all $x, y \in \mathbb{R}$, $t \in [0,T]$, and some constants $C, D > 0$:

1. $|c(t,x)| + |\sigma(t,x)| \leq C(1 + |x|)$.
2. $|c(t,x) - c(t,y)| + |\sigma(t,x) - \sigma(t,y)| \leq D|x - y|$.

Further, assume Z is a random variable independent of the σ-algebra generated by $B_s, s \geq 0$, such that

$$E[|Z|^2] < \infty.$$

Then the SDE

$$dX_t = c(t, X_t)dt + \sigma(t, X_t)dB_t$$

$$X_0 = Z$$

has a unique t-continuous solution X_t.

Proof: A proof can be found in [22, pp. 67-70].

So, using the notation in Theorem 4.2, we see that

$$\begin{aligned} c(t,x) &= (r - \gamma(t))x \\ \sigma(t,x) &= \sigma x \\ Z &= W_0. \end{aligned}$$

Thus, for any choice of $\gamma(t) \in M$, where M is as defined in Section 3.1, taking $C = D = r + \sigma$ clearly results in all of the hypotheses of Theorem 4.2 being satisfied. Hence, for any choice of $\gamma(t) \in M$, the SDE making up the first constraint has a unique solution.

Keeping all of this in mind, we can find that unique solution of (4.2) for our optimal controls found in Chapter 3, which is analogous to the solution found in the deterministic case:

Lemma 4.3: If $\gamma^*(t) = \kappa \bar{H}(t - d)$, where $d = d_A, d_A^*, d_P$, or d_P^*, whichever is relevant, and $W_0 > 0$ is a given constant, then the following stochastic process (strongly) solves (4.2) for all $t \in [0, T]$:

$$W_t = W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \int_0^t \gamma^*(s)ds + \sigma B_t\right).$$

Proof: To prove this, we will define

$$\begin{aligned} f_0(t,x) &= W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma x\right) \\ f_\kappa(t,x) &= W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \kappa(t-d) + \sigma x\right), \end{aligned}$$

where d is any of d_A, d_A^*, d_P, or d_P^*, whichever is relevant. We now show that the following equation is (uniquely) solved by $f_0(t, B_t)$ using Ito's formula:

$$dW_t = rW_t dt + \sigma W_t dB_t, t \in (0, d].$$

This problem is the same as (4.2) on the interval $[0, d]$. Next, we note the following:

$$\begin{aligned} \frac{\partial f_0}{\partial t} &= W_0\left(r - \frac{1}{2}\sigma^2\right)\exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma x\right) \\ \frac{\partial f_0}{\partial x} &= \sigma W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma x\right) \\ \frac{\partial^2 f_0}{\partial x^2} &= \sigma^2 W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma x\right). \end{aligned}$$

As a result, substituting $B_t = x$, then

$$\begin{aligned} \frac{\partial f_0}{\partial t} &= \left(r - \frac{1}{2}\sigma^2\right)W_t \\ \frac{\partial f_0}{\partial B_t} &= \sigma W_t \\ \frac{\partial^2 f_0}{\partial (B_t)^2} &= \sigma^2 W_t, \end{aligned}$$

where

$$W_t = f_0(t, B_t) = W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma B_t\right).$$

Thus, plugging these into Ito's formula, we find that

$$\begin{aligned} dW_t &= \left(\left(r - \frac{1}{2}\sigma^2\right)W_t + \frac{1}{2}\sigma^2 W_t\right)dt + \sigma W_t dB_t \\ &= rW_t dt + \sigma W_t dB_t. \end{aligned}$$

Since $f_0(0, 0) = W_0$ ($B_0 = 0$ by definition), then $f_0(t, B_t)$ uniquely solves (4.2) on $[0, d]$ by Theorems 4.1 and 4.2.

Next, assuming that this solution has been fully constructed (and hence a value for B_d is given), we consider the following problem on $[d, T]$:

$$\begin{aligned} dW_t &= (r - \kappa)W_t dt + \sigma W_t dB_t, t \in (d, T] \\ W_d &= W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)d + \sigma B_d\right), \end{aligned}$$

where B_d is the same value as that given by the distribution for the previous problem. This problem is the same as (4.2) on the interval $[d, T]$. Next, we note the following:

$$\begin{aligned} \frac{\partial f_\kappa}{\partial t} &= W_0\left(r - \frac{1}{2}\sigma^2 - \kappa\right)\exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \kappa(t - d) + \sigma x\right) \\ \frac{\partial f_\kappa}{\partial x} &= \sigma W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \kappa(t - d) + \sigma x\right) \\ \frac{\partial^2 f_\kappa}{\partial x^2} &= \sigma^2 W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \kappa(t - d) + \sigma x\right). \end{aligned}$$

As a result, substituting $B_t = x$, then

$$\begin{aligned}\frac{\partial f_0}{\partial t} &= \left(r - \frac{1}{2}\sigma^2 - \kappa\right) W_t \\ \frac{\partial f_0}{\partial B_t} &= \sigma W_t \\ \frac{\partial^2 f_0}{\partial (B_t)^2} &= \sigma^2 W_t,\end{aligned}$$

where

$$W_t = f_\kappa(t, B_t) = W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2 - \kappa\right) t - \kappa(t-d) + \sigma B_t\right).$$

Thus, plugging these into Ito's formula, we find that

$$\begin{aligned}dW_t &= \left(\left(r - \frac{1}{2}\sigma^2\right) W_t + \frac{1}{2}\sigma^2 W_t\right) dt + \sigma W_t dB_t \\ &= (r-\kappa) W_t dt + \sigma W_t dB_t.\end{aligned}$$

Since $f_\kappa(d, B_d) = W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right) d + \sigma B_d\right)$, which is independent of any information except that already provided by the previous problem, and, by [13, p. 215],

$$E[|f_\kappa(d, B_d)|^2] = W_0^2 \cdot \exp\left(2rd + \frac{3}{2}\sigma^2 d\right) < \infty,$$

then $f_\kappa(t, B_t)$ uniquely solves (4.2) on $[d, T]$ by Theorems 4.1 and 4.2.

Since the two solutions are equal at $t = d$, then, by Theorem 4.2, taking the solution defined by $f_0(t, B_t)$ on $[0, d]$ and joining it with the solution defined by $f_\kappa(t, B_t)$ on $[d, T]$ gives the unique solution of (4.2) on $[0, T]$. This completes the proof of Lemma 4.3.

4.2 Finding an Optimal Strategy

Next, we prove that $\gamma^*(t) = \kappa\bar{H}(t-d)$, where $d = d_A, d_A^*, d_P$, or d_P^*, whichever is relevant, solves (4.1-4.3). To do this, we will make use of stochastic versions of Theorems 3.1 and 3.2. First, we need some definitions and assumptions.

We begin by assuming that the only source of randomness in the problem is that generated by Standard Brownian Motion, B_t, and the controller (in our model, the plants via evolutionary forces) will know all relevant information up to the current time.

With this in mind, consider the following general optimization problem for $(t,x) \in [0,T] \times G$, where $G \subseteq \mathbb{R}$ and $W_0 \in G$ is given:

$$\text{Maximize} \quad E\left[K(W_T) + \int_0^T F(t, W_t, \gamma(t))dt\right] \tag{4.4}$$

$$\text{subject to} \quad dW_t = c(t, W_t, \gamma(t))dt + \sigma(t, W_t, \gamma(t))dB_t. \tag{4.5}$$

We define U to be the separable metric space (with metric d), which is also a convex set with nonempty interior, which gives the range of the control functions $\gamma(t) \in M$. Further, M is the set of all measurable, adapted Markov controls (that is, the value of $\gamma(t)$ for any $t \in [0,T]$ has no dependence on the value of $\gamma(s)$ for any $s < t$, but all information for any time prior to time t is available to the controller) such that $\gamma(t) \in U$ for all $t \in [0,T]$.

We further assume that $K(x), F(t,x,v), c(t,x,v), \sigma(t,x,v)$ are:

- measurable
- *twice* continuously differentiable with respect to x

- such that there exists a constant $C > 0$ such that, for any choice of x,

  $$|\phi(t, x, v)| \leq C(1 + |x|),$$

  where ϕ is any one of K, F, c, σ or their first partial derivatives with respect to x

- such that there is a constant $L > 0$ and a "modulus of continuity" $\omega : [0, \infty) \to [0, \infty)$ such that, taking ϕ to be any of K, F, c, σ,

  $$\begin{aligned} |\phi(t, x, v) - \phi(t, x^*, v^*)| &\leq L|x - x^*| + \omega(d(v, v^*)) \\ \left|\frac{\partial \phi}{\partial x}(t, x, v) - \frac{\partial \phi}{\partial x}(t, x^*, v^*)\right| &\leq L|x - x^*| + \omega(d(v, v^*)) \\ \left|\frac{\partial^2 \phi}{\partial x^2}(t, x, v) - \frac{\partial^2 \phi}{\partial x^2}(t, x^*, v^*)\right| &\leq \omega(|x - x^*| + d(v, v^*)) \end{aligned}$$

  for all $t \in [0, T]$, $x, x^* \in G$, $v, v^* \in U$

- such that c, F, σ are locally Lipschitz with respect to v, and their first partial derivatives with respect to x are continuous in (x, v).

We also require that, for any $W_0 \in G$, any choice of $\gamma(t) \in M$ implies $W_t \in G$ for all $t \in [0, T]$ (this means all possible controls are admissible). Since these, along with assuming B_t is the only source of randomness in the problem and the controller knows all relevant information up to the current time, will be the standard assumptions for (4.4-4.5), we will call this list (SA) for "stochastic assumptions." So, (SA) implies that any choice of $\gamma(t)$ will lead to a unique solution W_t of (4.5) by Theorem 4.2.

Once $\gamma(t)$ (and hence W_t) is chosen, we define the first-order *adjoint equation* to be:

$$dp(t) = -\left(\frac{\partial c}{\partial x}(t, W_t, \gamma(t))p(t) - \frac{\partial \sigma}{\partial x}(t, W_t, \gamma(t))q(t) + \frac{\partial F}{\partial x}(t, W_t, \gamma(t))\right) dt + q(t)dB_t$$
$$p(T) = \frac{\partial K}{\partial x}(W_T).$$

If (4.4-4.5) satisfies (SA), then there is a unique solution $(p(t), q(t))$ for a given $\gamma(t)$ and W_t (discussed in [27, pp. 347-354], but, more specifically, presented as Theorem 2.2 on p. 349 with proof on pp. 349-353).

However, for (4.4-4.5), there may be the need for a second-order adjoint equation; this occurs when $\sigma(t, x, v)$ has an explicit dependence on v, since the controller also has to worry about what will happen to the volatility when searching for an optimal control. In our problem, this does not happen, as our $\sigma(t, x, v)$ is not explicitly dependent on v. So, we only need the first-order adjoint equation to proceed.

From this, we define the following function:

$$H(t, x, v, p, q) = p(t)c(t, x, v) + q(t)\sigma(t, x, v) + F(t, x, v),$$

which is the *Hamiltonian* for (4.4-4.5). As in the deterministic case, it will play an important role in our necessary and sufficient conditions for optimality. We begin with a necessary condition, which is taken from Theorem 3.2 (also called the (Pontryagin) Maximum Principle) in Yong-Zhou ([27, p. 103]):

Theorem 4.4: Assume (4.4-4.5) satisfies (SA), and assume that $\sigma(t, x, v)$ has no explicit dependence on v. If $\gamma^*(t)$ is an optimal control with corresponding constraint solution W_t^* and (first-order) adjoint solution $(p(t), q(t))$, then

$$H(t, W^*(t), \gamma^*(t), p(t), q(t)) = \max_{v \in U} H(t, W^*(t), v, p(t), q(t))$$

for almost every $t \in [0, T]$, almost surely.

Proof: A proof can be found in ([27, pp. 124-137]). However, the given proof can be greatly simplified in this case because a second-order adjoint equation is not needed.

Next, we give a sufficient condition for optimality:

Theorem 4.5: Assume (4.4-4.5) satisfies (SA), and assume that $\sigma(t, x, v)$ has no explicit dependence on v. Let $\gamma^*(t) \in M$, W_t^* be the corresponding constraint solution, and $(p(t), q(t))$ be the corresponding (first-order) adjoint solution. If:

1. K is concave
2. For any other choice of $\gamma(t) \in M$ and corresponding W_t,

   $$H(t, W_t, \gamma(t), p(t)) - H(t, W_t^*, \gamma^*(t), p(t)) \leq \frac{\partial H}{\partial x}(t, W_t^*, \gamma^*(t), p(t)) \cdot (W_t - W_t^*)$$

   for all $t \in [0, T]$,

then $\gamma^*(t)$ is an optimal control.

Proof: The proof will largely follow that of Theorem 3.2. As in that proof, we begin by defining $\xi(t) = W_t - W_t^*$. By assumption, $\xi(t)$ satisfies:

$$d\xi(t) = \left(\frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + \alpha(t)\right) dt + \left(\frac{\partial \sigma}{\partial x}(t, W^*(t), \gamma^*(t)) \cdot \xi(t) + \beta(t)\right) dB_t$$
$$\xi(0) = 0,$$

where

$$\alpha(t) = -\frac{\partial c}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + c(t, W_t, \gamma(t)) - c(t, W_t^*, \gamma^*(t))$$
$$\beta(t) = -\frac{\partial \sigma}{\partial x}(t, W_t^*, \gamma^*(t)) \cdot \xi(t) + \sigma(t, W_t, \gamma(t)) - \sigma(t, W_t^*, \gamma^*(t)).$$

With this in mind, along with the given assumptions and the useful results (collected from [22, p. 30 and p. 55], respectively)

$$E\left[\int_a^b f(t)dB_t\right] = 0$$

$$d(X_tY_t) = X_tdY_t + dX_tY_t + dX_t \cdot dY_t$$

for any Ito processes X_t, Y_t and $L^2([a,b])$-measurable function f, we then note the following:

$$
\begin{aligned}
E\left[\frac{\partial K}{\partial x}(W_T^*)\cdot\xi(T)\right] &= E[p(T)\xi(T)-p(0)\xi(0)]\\
&= E\left[\int_0^T \left(-\left(\frac{\partial c}{\partial x}(t,W_t^*,\gamma^*(t))p(t)\right.\right.\right.\\
&\qquad\qquad \left.-\frac{\partial \sigma}{\partial x}(t,W_t^*,\gamma^*(t))q(t)+\frac{\partial F}{\partial x}(t,W_t^*,\gamma^*(t))\right)\xi(t)\\
&\qquad +p(t)\left(\frac{\partial c}{\partial x}(t,W_t^*,\gamma^*(t))\cdot\xi(t)+\alpha(t)\right)\\
&\qquad \left.\left.+q(t)\left(\frac{\partial \sigma}{\partial x}(t,W^*(t),\gamma^*(t))\cdot\xi(t)+\beta(t)\right)\right)dt\right]\\
&= E\left[\int_0^T \left(-\frac{\partial F}{\partial x}(t,W_t^*,\gamma^*(t))\cdot\xi(t)+p(t)\alpha(t)+q(t)\beta(t)\right)dt\right]\\
&= E\left[\int_0^T \left(-\frac{\partial H}{\partial x}(t,W_t^*,\gamma^*(t),p(t))\cdot\xi(t)\right.\right.\\
&\qquad + p(t)\cdot\frac{\partial c}{\partial x}(t,W_t^*,\gamma^*(t))\cdot\xi(t)\\
&\qquad + q(t)\cdot\frac{\partial \sigma}{\partial x}(t,W^*(t),\gamma^*(t))\\
&\qquad \left.\left.+ p(t)\alpha(t)+q(t)\beta(t)\right)dt\right]\\
&= E\left[\int_0^T \left(-\frac{\partial H}{\partial x}(t,W_t^*,\gamma^*(t),p(t))\cdot(W_t-W_t^*)\right.\right.\\
&\qquad + p(t)(c(t,W_t,\gamma(t))-c(t,W_t^*,\gamma^*(t)))\\
&\qquad \left.\left.+ q(t)(\sigma(t,W_t,\gamma(t))-\sigma(t,W_t^*,\gamma^*(t)))\right)dt\right]\\
&\le E\left[\int_0^T (H(t,W_t^*,\gamma^*(t),p(t))-H(t,W_t,\gamma(t),p(t))\right.\\
&\qquad +p(t)(c(t,W_t,\gamma(t))-c(t,W_t^*,\gamma^*(t)))\\
&\qquad \left.+q(t)(\sigma(t,W_t,\gamma(t))-\sigma(t,W_t^*,\gamma^*(t))))\,dt\right]\\
&= E\left[\int_0^T (F(t,W^*(t),\gamma^*(t))-F(t,W_t,\gamma(t)))\,dt\right].
\end{aligned}
$$

The expected value in the second line was simplified using the two given results, neglecting the terms with differential pieces $(dt)^2$ and $dt \cdot dB_t$ (these are assumed to be much smaller than the other terms), and using the fact that $dB_t \cdot dB_t = dt$ ([22, p. 44]).

Since $K(x)$ is assumed concave and $C^2(G)$, then

$$E\left[\frac{\partial K}{\partial x}(W_T^*) \cdot (W_T - W_T^*)\right] \geq E\left[K(W_T) - K(W_T^*)\right].$$

Tying this all together, we then have

$$E\left[K(W_T) + \int_0^T F(t, W_t, \gamma(t))dt\right] \leq E\left[K(W_T^*) + \int_0^T F(t, W_t^*, \gamma^*(t))dt\right].$$

Since $\gamma(t) \in M$ was arbitrary, this completes the proof of Theorem 4.5.

Remark: This theorem was adapted from Theorem 5.2 in Yong-Zhou ([27, pp. 138-140]) because, as in the deterministic case, our $H(t, x, v, p, q)$ is not concave in (x, v), which is needed in order to turn Theorem 4.4 into an if-and-only-if statement.

So, with Theorems 4.4 and 4.5, we are now ready to find some optimal controls. First, for (4.1-4.3), we note that we have $G = [0, \infty)$ and $U = [0, \kappa]$ (with metric $|\cdot|$) again. Further,

$$\begin{aligned} c(t, x, v) &= (r - v)x \\ F(t, x, v) &= bxv \\ K(x) &= ax \\ \sigma(t, x) &= \sigma x. \end{aligned}$$

These functions clearly satisfy (SA) (in fact, c, F, σ are actually Lipschitz in v, not just locally Lipschitz). So, we then set up the first-order adjoint equation, which is:

$$dp(t) = ((\gamma(t) - r)p(t) + \sigma q(t) - b\gamma(t))\,dt + q(t)dB_t$$
$$p(T) = a.$$

It can quickly be verified that, setting $q(t) = 0$, the adjoint equation reduces to the same adjoint equation as in the deterministic case (3.1-3.3), and so the solution of this equation is $(p^*(t), 0)$, where

$$p^*(t) = a \cdot \exp\left(r(T-t) - \int_t^T \gamma(s)ds\right) + b\int_t^T \gamma(s) \cdot \exp\left(r(s-t) - \int_t^s \gamma(u)du\right) ds.$$

Since the Hamiltonian for (4.1-4.3) is

$$H(t, W_t, \gamma(t), p(t), q(t)) = W_t(rp(t) + \gamma(t)(b - p(t)) + \sigma q(t)),$$

then, by above, the Hamiltonian reduces to the same form as in the deterministic case. Hence, by Theorems 4.4 and 4.5, we have the following:

Theorem 4.6: Theorem 3.3, Lemma 3.4, and Theorem 3.5 still hold in the stochastic case. That is,

- If $a = 0$, then $\gamma^*(t) = \kappa\bar{H}(t - d_A)$ (or d_A^* if $r = \kappa$) is an optimal control.
- If $a > 0$ and $b/a \leq 1$, then $\gamma^*(t) = 0$ is an optimal control.
- If $a > 0$ and $b/a > 1$, then $\gamma^*(t) = \kappa\bar{H}(t - d_P)$ (or d_P^* if $r = \kappa$) is an optimal control.

Proof: The proof is the same as the proofs for Theorem 3.3, Lemma 3.4, and Theorem 3.5, respectively, by the above discussion.

Remark 1: Just for reference, here is the general form of the second-order adjoint equation for the stochastic optimization problem:

$$\begin{aligned} dP(t) = &-\left(2P(t)\frac{\partial c}{\partial x}(t, W_t, \gamma(t)) + P(t)\left(\frac{\partial \sigma}{\partial x}(t, W_t, \gamma(t))\right)^2 + 2Q(t)\frac{\partial \sigma}{\partial x}(t, W_t, \gamma(t))\right) \\ &- \frac{\partial^2 H}{\partial x^2}(t, W_t, \gamma(t), p(t), q(t))dt + Q(t)dB_t \\ P(T) = &\frac{\partial^2 K}{\partial x^2}(W_T). \end{aligned}$$

It can easily be verified that $(P(t), Q(t)) = (0, 0)$ is a solution of this equation for our problem, and, since this equation has a unique solution $(P(t), Q(t))$ (Theorem 2.2 in [27, p. 349]), this confirms that there is no need for a second adjoint equation for our problem.

Remark 2: Recall that, in the deterministic case, we computed the corresponding optimal values for each optimal control. These will also be the corresponding optimal values in the stochastic case because of Jensen's Inequality ([10, p. 109]). One of the forms of Jensen's Inequality is that, if X is an integrable, real-valued random variable (meaning that, equivalently, $E[|X|] < \infty$), and ϕ is a convex function, then

$$\phi(E[X]) \leq E[\phi(X)].$$

If ϕ is concave, then the inequality reverses. Hence, if ϕ is both convex and concave, then Jensen's Inequality becomes an equality. In our case, we take

$$X(t) = W_t = W_0 \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \int_0^t \gamma^*(s)ds + \sigma B_t\right),$$

where $\gamma^*(t) = \kappa\bar{H}(t - d)$, where d is the appropriate starting time for reproduction,

and

$$\phi(x(t)) = \int_0^T \gamma^*(t)x(t)dt.$$

Clearly, ϕ is a linear function in $x(t)$, and hence it is both convex and concave. Now, by [13, p. 215], for any value of t,

$$E[|X(t)|] = E[X(t)] = W_0 \cdot \exp\left(rt - \int_0^t \gamma^*(s)ds\right).$$

Thus, Jensen's Inequality becomes an equality in our case, and we have that:

$$\begin{aligned} &E\left[aW_T + b\int_0^T \gamma^*(t)W_t dt\right] \\ &= aE[W_T] + b\int_0^T \gamma^*(t)E[W_t]dt \\ &= aW_0 \cdot \exp\left(rT - \kappa(T-d)\right) + bW_0\kappa \int_d^T \exp\left(rt - \kappa(t-d)\right)dt. \end{aligned}$$

Therefore, the optimal values in the stochastic case are indeed the same as those in the deterministic case.

Initially, this may seem quite strange, as the optimal strategies and corresponding values are completely unchanged from the deterministic case. This is due to the fact that we are maximizing an expected value, and, since B_t has independent normally distributed increments with mean 0, then this is essentially equivalent to the effects of the environment "breaking even" in the long run.

This then implies that all of the other results we derived for the deterministic case carry over to the stochastic case.

Chapter 5

Multiseason Analysis

We will now look at what happens to these plant populations over a large number of seasons; specifically, we want to answer two questions:

1. What condition(s) will ensure that the population will grow over a long period of time?
2. Under what condition(s) will perennials be favored? What about annuals?

To do this, we assume that, as a result of evolution, the plants use the optimal reproductive strategies $\gamma^*(t)$ already derived in previous sections. With this in mind, we define the following stochastic processes for $t \in [0, T]$ and $n = 0, 1, 2, \ldots$:

$$\begin{aligned} W_t^{(n)} &= W_0^{(n)} \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2 \right) t - \int_0^t \kappa \bar{H}(s-d)ds + \sigma B_t \right) \\ W_0^{(n)} &= aW_T^{(n-1)} + b\int_0^T \kappa \bar{H}(s-d) W_s^{(n-1)} ds \\ W_0^{(0)} &= W_0, \end{aligned}$$

where d is the time where reproduction begins as derived in previous sections (whichever of d_A, d_A^*, d_P, or d_P^* is appropriate). So, note that $W_t^{(n)}$ is a continuous stochastic process in t for fixed n (this represents the dynamics of the plants during the n^{th} season), and $W_0^{(n)}$ is a discrete stochastic process in n. This represents the adult biomass that will exist at the start of the n^{th} season under the chosen reproductive strategy; recall that we are assuming that any reproductive biomass which will germinate into a full-grown adult will have done so by the start of the next season.

In order to see what will happen with the plant species over a large number of seasons, we want to investigate $W_0^{(n)}$ as n becomes very large. To do this, we first want to rewrite this sequence in a simpler fashion. Specifically, assuming that each season's dynamics are independent of those of other seasons, then, calling

$$\begin{aligned} Y_t &= \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \int_0^t \kappa\bar{H}(s-d)ds + \sigma B_t\right) \\ X_n &= aY_T + b\int_0^T \kappa\bar{H}(s-d)Y_s ds, \end{aligned}$$

we can then say that

$$W_0^{(n)} = W_0 X_1 \cdots X_n.$$

Further, W_0 is a positive constant, and the X_i's are independent and identically distributed (i.i.d.) random variables. The X_i's are also continuous random variables which take on values in the interval $(0, \infty)$. With this in mind, we notice that the population will be considered to have grown after n seasons (that is, $W_0^{(n)} > W_0$) so long as the product $X_1 \cdots X_n > 1$. Likewise, the population will be considered to have decayed after n seasons if $X_1 \cdots X_n < 1$. To determine under what conditions growth is more likely to occur than decay, we need to look at the distribution of $W_0^{(n)}$, and we will do so in three cases:

1. $a > 0$, $b/a \leq 1$
2. $a = 0$

3. $a > 0$, $b/a > 1$.

5.1 Case 1: $a > 0$, $b/a \leq 1$

We begin with the easiest of the cases to analyze since, in this case, the optimal "reproductive strategy" for the perennial plants is to focus all available resources on growth and maintenance of the existing adult population rather than reproduce, or, mathematically, $\gamma^*(t) = 0$ (Lemma 3.4). This is equivalent to saying that $d_P = T$ (remark after Theorem 3.5), and so we have

$$\begin{aligned} Y_t &= \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma B_t\right) \\ X_n &= aY_T \\ &= a \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)T + \sigma B_T\right). \end{aligned}$$

Next, we note the following:

$$\begin{aligned} \ln(W_0^{(n)}) &= \ln(W_0) + \ln(X_1) + \ldots + \ln(X_n) \\ \ln(X_n) &= \ln a + \left(r - \frac{1}{2}\sigma^2\right)T + \sigma B_T. \end{aligned}$$

So, because the X_i's are i.i.d. random variables, and B_T is a normally distributed random variable, then so is $\ln(W_0^{(n)})$ because it is a sum of normally distributed random variables. This means that $W_0^{(n)}$ is a lognormally distributed random variable. One could also get this by noting that the X_i's are lognormally distributed and $W_0^{(n)}$ is a product of lognormally distributed random variables. But, we still need to figure out its mean and variance, and we'll use the above expression for $\ln(W_0^{(n)})$ to do so.

Recalling that $E[B_T] = 0$ and $\mathrm{Var}(B_T) = T$ by definition, we have the following:

$$\begin{aligned}\mu &= E[\ln(W_0^{(n)})] = \ln(W_0) + n\left(\ln a + \left(r - \frac{1}{2}\sigma^2\right)T\right)\\ \nu^2 &= \mathrm{Var}(\ln(W_0^{(n)})) = n\sigma^2 T.\end{aligned}$$

Also note that, if X is any lognormally distributed random variable such that $\ln X$ has mean μ and variance ν^2, then, by [17, p. 113],

$$\begin{aligned}E[X] &= \exp\left(\mu + \frac{1}{2}\nu^2\right)\\ \mathrm{Var}(X) &= (E[X])^2\left(\exp(\nu^2) - 1\right).\end{aligned}$$

As a result, for any value of n, we have that

$$\begin{aligned}E[W_0^{(n)}] &= W_0 a^n \cdot \exp(nrT)\\ \mathrm{Var}(W_0^{(n)}) &= (W_0 a^n \cdot \exp(nrT))^2(\exp(n\sigma^2 T) - 1).\end{aligned}$$

We want to determine how likely $X_1 \cdots X_n > 1$ for a given value of n; that is, what is the probability that the population has grown over n seasons? For this to happen with at least 50% certainty for any n, by above, we need

$$\begin{aligned}E[\ln(X_1) + \ldots + \ln(X_n)] = n\left(\ln a + \left(r - \frac{1}{2}\sigma^2\right)T\right) &> 0\\ a &> \exp\left(-\left(r - \frac{1}{2}\sigma^2\right)T\right).\end{aligned}$$

Biologically, this says that, in order to have long-term population growth occur a majority of the time, the average amount of the adult biomass that survives from one season to the next must be large enough so that the growth for a season is not offset (the $\exp(-rT)$ piece) and neither are the expected adverse effects of environmental variability for a season (the $\exp\left(\frac{1}{2}\sigma^2 T\right)$ piece). We also make the important observation that determining whether growth is more likely than decay after any number of seasons is independent of the number of seasons.

In fact, in this case, we can get more accurate results than this. For any choice of n, we can get a more exact estimate for how likely the population will grow after n seasons because we know that

$$\ln(X_1) + \ldots + \ln(X_n) \sim N\left(\ln(W_0) + n\left(\ln a + \left(r - \frac{1}{2}\sigma^2\right)T\right), n\sigma^2 T\right).$$

So, we can use a normal distribution table to find $P(\ln(X_1) + \ldots \ln(X_n) > 0)$, and this will then correspond to $P(X_1 \cdots X_n > 1)$.

If we wanted to answer other interesting questions such as the likelihood of the population having at least doubled in season n or having been cut in half (or worse) in season n, we could use a very similar technique. For example, the likelihood of the population having at least doubled by season n corresponds to $P(\ln(X_1) + \ldots + \ln(X_n) > \ln(2))$.

Remark: Although this case lends itself very nicely to mathematical analysis, it is, of course, not viable in the long run, as, if n is sufficiently large, the population must eventually die out since it never reproduces. Thus, the above should only be used for small values of n to ensure a realistic analysis.

5.2 Case 2: $a = 0$

5.2.1 Derivation of a Sufficient Growth Condition

Our next case to consider is the case of annuals; that is, reproduction always occurs at some point during the season. In this case, we have

$$X_n = b\kappa \int_{d_A}^{T} \exp\left(\left(r - \frac{1}{2}\sigma^2\right) s - \kappa(s - d_A) + \sigma B_s\right) ds,$$

where

$$d_A = \begin{cases} T - \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right) & r \neq \kappa \\ T - \frac{1}{\kappa} & r = \kappa \end{cases}$$

taking $d_A = 0$ if the appropriate value above is less than 0 (for distinction, we'll set $d_A^* = T - \frac{1}{\kappa}$ as before). However, unlike Case 1, since this is the integral of a lognormally distributed random variable, we can't simply claim that $\ln(X_n)$ is normally distributed. Since

$$\ln(W_0^{(n)}) = \ln(W_0) + \ln(X_1) + \ldots + \ln(X_n),$$

then, by the Central Limit Theorem (see, for example, [13, p. 308]), we know that, for sufficiently large n, $\ln(W_0^{(n)})$ is approximately normally distributed, and hence $W_0^{(n)}$ is approximately lognormally distributed for sufficiently large n. Thus, for sufficiently large n, we can proceed as in Case 1. However, we have to do things in "reverse;" that is, we'll first need to work with X_n instead of $\ln(X_n)$.

First, recall that, by Remark 2 after Theorem 4.6, we know that

$$E[X_n] = \begin{cases} \frac{b\kappa}{r-\kappa}\left(\exp(rT - \kappa(T-d_A)) - \exp(rd_A)\right) & r \neq \kappa \\ b \cdot \exp(\kappa d_A^*) & r = \kappa \end{cases}.$$

Next, we turn to computing $\mathrm{Var}(X_n)$; this is much more difficult to do than in Case 1 due to X_n being an integral of a random variable. But, we can get an upper bound on the integral; namely, we note that, for any choice of sample path of B_t, the following inequality holds for $t \in [0, T]$:

$$\bar{H}(t-d_A) \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \kappa(t-d_A) + \sigma B_t\right) \leq \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma B_t\right).$$

So, calling

$$X_n^* = b\kappa \int_0^T \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t + \sigma B_t\right), \tag{5.1}$$

we then have $X_n \leq X_n^*$ for any path of Standard Brownian Motion, and hence

$$\mathrm{Var}(X_n) = E[X_n^2] - E[X_n]^2 \leq E[(X_n^*)^2] - E[X_n]^2.$$

Now, to compute $E[(X_n^*)^2]$, we turn to Corollary 2 from Yor ([28, p. 519]), which says the following:

Lemma 5.1: For any $\lambda \in \mathbb{R}$, $\alpha \in \mathbb{R}$, and $n = 1, 2, \ldots$,

$$E\left[\left(\int_0^T \exp(\lambda(B_t + \alpha t))dt\right)^n\right] = \frac{n!}{\lambda^{2n}} \sum_{j=0}^{n} c_j^{(\alpha/\lambda)} \cdot \exp\left(\left(\frac{\lambda^2 j^2}{2} + \lambda j \alpha\right)T\right),$$

where

$$c_j^{(x)} = \prod_{k=0,k\neq j}^{n} \left(\frac{(x+j)^2}{2} - \frac{(x+k)^2}{2} \right)^{-1}.$$

Proof: The proof can be constructed in a straightforward manner using results on pp. 510 and 517-519 of Yor ([28]). Since doing so requires 3 prior results from [28] and Girsanov's Theorem (see, for example, [22, pp. 153-160]), for the sake of brevity, we will omit the proof.

Thus, taking $\lambda = \sigma$ and $\alpha = r/\sigma - (1/2)\sigma$, we have $\alpha/\lambda = r/\sigma^2 - 1/2$, and hence, by Lemma 5.1,

$$\begin{aligned} E[(X_n^*)^2] &= \frac{2b^2\kappa^2}{\sigma^4}\left(\left(\frac{-r}{\sigma^2}\right)^{-1} \left(\frac{-2r}{\sigma^2} - 1\right)^{-1} + \left(\frac{r}{\sigma^2}\right)^{-1} \left(\frac{-r}{\sigma^2} - 1\right)^{-1} \exp(rT) \right. \\ &\qquad \left. + \left(\frac{2r}{\sigma^2} + 1\right)^{-1} \left(\frac{r}{\sigma^2} + 1\right)^{-1} \exp((2r+\sigma^2)T) \right) \\ &= 2b^2\kappa^2 \left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(rT)}{r(r+\sigma^2)} + \frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)} \right). \end{aligned}$$

So, as a result assuming $r \neq \kappa$,

$$\begin{aligned} \mathrm{Var}(X_n) \leq 2b^2\kappa^2 &\left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(rT)}{r(r+\sigma^2)} + \frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)} \right) \\ &- \left(\frac{b\kappa}{r-\kappa} \left(\exp(rT - \kappa(T-d_A)) - \exp(rd_A)\right) \right)^2. \end{aligned}$$

Next, we note that, because the X_i's are i.i.d. random variables, then

$$\begin{aligned} E[X_1 \cdots X_n] &= (E[X_n])^n \\ \mathrm{Var}(X_1 \cdots X_n) &= (E[X_n^2])^n - (E[X_n])^{2n} \\ &\leq (E[(X_n^*)^2])^n - (E[X_n])^{2n}. \end{aligned}$$

This then gives us a "worst-case scenario" for analyzing whether the population will grow or not after a sufficiently large number of seasons. To illustrate this, we first note that, if we know the mean and variance of a lognormally distributed random variable X, then we can compute μ and ν^2, the mean and variance of the corresponding normally distributed random variable $\ln(X)$, respectively, via the following formulas (these can be verified by plugging them into the formulas for $E[X]$ and $\operatorname{Var}(X)$ in Section 5.1):

$$\begin{aligned}\mu &= \ln(E[X]) - \frac{1}{2}\ln\left(1 + \frac{\operatorname{Var}(X)}{E[X]^2}\right)\\ \nu^2 &= \ln\left(1 + \frac{\operatorname{Var}(X)}{E[X]^2}\right).\end{aligned}$$

Since we computed an upper bound for $\operatorname{Var}(X_1 \cdots X_n)$, then, by the above formulas, the corresponding μ and ν^2 for that lognormal distribution will be, respectively, less than and greater than the true μ and ν^2. Put another way, the underlying normal distribution of the "worst-case scenario" will have a smaller mean and greater variance than the true underlying normal distribution.

As a result, if we can find a condition on the "worst-case scenario" distribution's underlying normal distribution that guarantees its mean (and hence the median of the "worst-case scenario's" distribution by [17, p. 117]) is at least 0, then the true median is at least that big, if not bigger. So, for the true distribution, there is at least a 50% chance of growth in each season. Using the "worst-case scenario" distribution to do other computations, though, may not be feasible; we'll discuss this a little more at the end of this section.

With this in mind, let's return to analyzing the distribution of $X_1 \cdots X_n$. Specifically, assuming n is sufficiently large, then we can compute the corresponding mean and variance of the underlying normal distribution of the "worst-case scenario," μ^*

and $(\nu^*)^2$, respectively (μ and ν^2 represent the true values), as follows:

$$\begin{aligned}
\nu^2 &= \ln\left(1 + \frac{\operatorname{Var}(X_1 \cdots X_n)}{E[X_1 \cdots X_n]^2}\right) \\
&\leq \ln\left(\frac{E[(X_n^*)^2]^n}{E[X_n]^{2n}}\right) \\
&= (\nu^*)^2 \\
(\nu^*)^2 &= n \ln\left(2(r-\kappa)^2\left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(rT)}{r(r+\sigma^2)} + \frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)\right) \\
&\quad + n \ln\left((\exp(rT - \kappa(T - d_A)) - \exp(rd_A))^{-2}\right) \\
\mu &= \ln(E[X_1 \cdots X_n]) - \frac{1}{2}\nu^2 \\
&\geq \ln(E[X_n]^n) - \frac{1}{2}(\nu^*)^2 \\
&= \mu^* \\
\mu^* &= n \ln\left(\frac{b\kappa}{\sqrt{2}(r-\kappa)^2}(\exp(rT - \kappa(T - d_A)) - \exp(rd_A))^2\right) \\
&\quad + n \ln\left(\left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(rT)}{r(r+\sigma^2)} + \frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{-1/2}\right).
\end{aligned}$$

Thus, if we want to guarantee long-term population growth for these annuals at least 50% of the time, we want μ^* to be greater than 0, or, equivalently, $\exp(\mu^*) > 1$ ([17,

p. 117]); for this to happen, we need:

$$\begin{aligned}
&\left(\frac{b\kappa}{\sqrt{2}(r-\kappa)^2}\right)^n (\exp(rT-\kappa(T-d_A))-\exp(rd_A))^{2n} \\
&\cdot\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{-n/2} > 1 \\
b &> \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT-\kappa(T-d_A))-\exp(rd_A))^{-2} \\
&\cdot\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{1/2} \\
b &> \frac{\sqrt{2}(r-\kappa)^2}{\kappa}\exp(-2rT)\left(\left(\frac{r}{\kappa}\right)^{-\frac{\kappa}{r-\kappa}}-\left(\frac{r}{\kappa}\right)^{-\frac{r}{r-\kappa}}\right)^{-2} \\
&\cdot\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{1/2},
\end{aligned}$$

where the last inequality was obtained by plugging in d_A, which is dependent only on r, κ, T. This assumes, of course, that d_A is positive; if $d_A = 0$, the inequality becomes:

$$\begin{aligned}
b &> \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT-\kappa T))^{-2} \\
&\cdot\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{1/2}.
\end{aligned}$$

So, defining

$$f(r,\sigma,T)=\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{1/2},$$

then we can write this sufficient growth condition as:

$$b > \begin{cases} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT-\kappa T))^{-2}\cdot f(r,\sigma,T) & T \leq \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right) \\ \frac{\sqrt{2}(r-\kappa)^2}{\kappa}\exp(-2rT)\left(\left(\frac{r}{\kappa}\right)^{-\frac{\kappa}{r-\kappa}}-\left(\frac{r}{\kappa}\right)^{-\frac{r}{r-\kappa}}\right)^{-2}\cdot f(r,\sigma,T) & T \geq \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right) \end{cases}. \tag{5.2}$$

However, if $r = \kappa$, note that all we need to do in the above computations is replace $E[X_n]$ with $b\kappa(T - d_A^*) \cdot \exp(\kappa d_A^*)$ and r with κ in $E[(X_n^*)^2]$; otherwise, everything else remains the same. Thus, in this case,

$$\begin{aligned}
(\nu^*)^2 &= n \ln\left(2(T - d_A^*)^{-2} \exp(-2\kappa d_A^*)\right) \\
&\quad + n \ln\left(\frac{1}{\kappa(2\kappa + \sigma^2)} - \frac{\exp(\kappa T)}{\kappa(\kappa + \sigma^2)} + \frac{\exp((2\kappa + \sigma^2)T)}{(2\kappa + \sigma^2)(\kappa + \sigma^2)}\right) \\
\mu^* &= n \ln\left(\frac{b\kappa}{\sqrt{2}}(T - d_A^*)^2 \exp(2\kappa d_A^*)\right) \\
&\quad + n \ln\left(\left(\frac{1}{\kappa(2\kappa + \sigma^2)} - \frac{\exp(\kappa T)}{\kappa(\kappa + \sigma^2)} + \frac{\exp((2\kappa + \sigma^2)T)}{(2\kappa + \sigma^2)(\kappa + \sigma^2)}\right)^{-1/2}\right).
\end{aligned}$$

So, if $r = \kappa$, to guarantee long-term growth at least 50% of the time, we want

$$b > \begin{cases} \frac{\sqrt{2}}{\kappa T^2} \cdot f(\kappa, \sigma, T) & T \leq \frac{1}{\kappa} \\ \kappa\sqrt{2} \cdot \exp(2 - 2\kappa T) \cdot f(\kappa, \sigma, T) & T \geq \frac{1}{\kappa} \end{cases}. \tag{5.3}$$

Remark 1: To derive (5.1), note that all terms involving κ were essentially dropped in the integrand. This is because determining when the κ term in the exponent normally begins depends on d_A; if $d_A > 0$, then leaving it as $\kappa(t - d_A)$ does give a valid upper bound, but it may be worse than (5.1), especially if d_A is not close to 0. This is because terms would be *added* to the exponent, not taken away, close to 0.

Also, the change made to $E[(X_n^*)^2]$ would be to replace r with $(r - \kappa)$, and so, if $r < \kappa$, then it becomes possible for denominators to be equal to 0, depending on the value of σ^2. So, to avoid this possible complication, and to create a universal bound that would be valid regardless of the values of r and κ, we simply decided to drop the terms in the integrand involving κ.

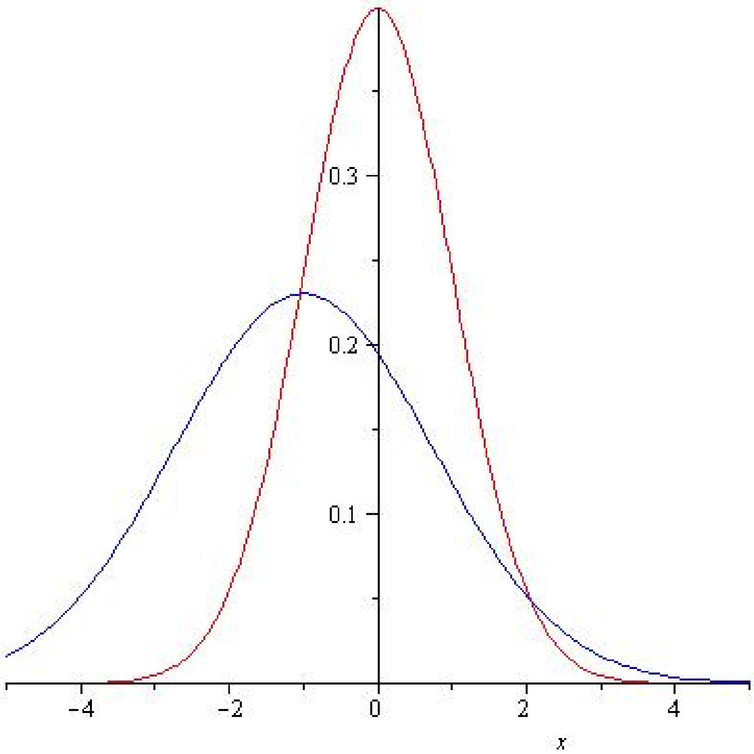

Figure 5.1: Comparison of two normal distributions (red has mean 0 and variance 1, blue has mean -1 and variance 3)

Remark 2: As pointed out earlier, using the "worst-case scenario" for other computations besides a sufficient condition for season-to-season as well as long-term growth may not be feasible. To see why, let's take two normally-distributed random variables, $A \sim N(\mu_1, \nu_1^2)$ and $B \sim N(\mu_2, \nu_2^2)$, where $\mu_1 \geq \mu_2$ and $\nu_1 \leq \nu_2$. So, here, B is our "worst-case scenario" distribution. Figure 5.1 illustrates this, with the red curve representing the true distribution, A, and the blue curve representing the "worst-case scenario," B.

If we wanted to use B to talk about what's going on with A, there are instances where B rightfully deserves the name "worst-case scenario." For example, if we wanted to compute $P(A > x_1)$, where $\mu_2 \leq x_1 \leq \mu_1$, then $P(B > x_1)$ does give a lower answer than $P(A > x_1)$. To see why, we quickly note that $x_1 - \mu_2 \leq 0$ and $x_1 - \mu_1 \geq 0$ and hence

$$\frac{x_1 - \mu_2}{\nu_2} \leq \frac{x_1 - \mu_1}{\nu_1}.$$

So, in this case, calling B the "worst-case scenario" is justified. This corresponds to the region $-1 \leq x \leq 0$ in Figure 5.1; clearly, if x is in this region, then $P(B > x) < P(A > x)$ since the mean represents the median for both distributions.

On the other hand, if we wanted to look at $P(A > x_2)$, where $x_2 \leq \mu_2$ or $x_2 \geq \mu_1$, then the relationship of $P(B > x_2)$ to $P(A > x_2)$ is not as clear. To see why, we note that there is a value of x_2 where the standardized normal distributions for A and B will produce the same values for the probabilities; this happens when:

$$\begin{aligned}
\frac{x_2 - \mu_1}{\nu_1} &= \frac{x_2 - \mu_2}{\nu_2} \\
\frac{x_2}{\nu_1} - \frac{x_2}{\nu_2} &= \frac{\mu_1}{\nu_1} - \frac{\mu_2}{\nu_2} \\
\frac{x_2(\nu_2 - \nu_1)}{\nu_1\nu_2} &= \frac{\mu_1\nu_2 - \mu_2\nu_1}{\nu_1\nu_2} \\
x_2 &= \frac{\mu_1\nu_2 - \mu_2\nu_1}{\nu_2 - \nu_1}.
\end{aligned}$$

Further, we note that this value is bigger than μ_1 since

$$\begin{aligned}
\frac{\mu_1\nu_2 - \mu_2\nu_1}{\nu_2 - \nu_1} &\geq \mu_1 \\
\mu_2\nu_1 &\leq \mu_1\nu_1 \\
\mu_2 &\leq \mu_1,
\end{aligned}$$

which is true by assumption. Hence, we see that, if $x_2 \leq \mu_2$, then $P(B > x_2)$ does again provide a lower estimate for $P(A > x_2)$, so the "worst-case scenario" label is justified again. This is illustrated in Figure 5.1 in the region $x < -1$; not only is the median of A to the right of that of B, but, since the variance of A is smaller, then more of its area is contained near the median compared to B. However, if $x_2 \geq \mu_1$, then $P(B > x_2)$ only provides a lower estimate for $P(A > x_2)$ up until

$$x_2 = \frac{\mu_1\nu_2 - \mu_2\nu_1}{\nu_2 - \nu_1},$$

after which $P(B > x_2)$ provides an *upper* estimate for $P(A > x_2)$. For Figure 5.1, this critical value is $x = 1/2$.

In summary, returning to the distributions analyzed in Case 2, where the mean and variance of the true underlying normal distribution are not necessarily known, using the "worst-case scenario" distribution to get a lower estimate for the true distribution for computations of the form $P(X > x)$ should only be done if x is less than the mean of the underlying normal distribution of the "worst-case scenario," μ^*. Although there may be no harm in looking at $P(B > x)$ to get a lower bound on $P(A > x)$ if x is only very slightly greater than μ^*, this should only be done if necessary, especially since the comparison to the true distribution is not as clear in this case.

5.2.2 A Few Graphs

We now look at some graphs to help determine what roles the parameters r, κ, T, and σ play in terms of how high the reproductive utility, b, must be to ensure that the sufficient condition for growth at least 50% of the time derived in the previous section, (5.2) or (5.3), is met. We'll look at the case $r \neq \kappa$ first and then discuss what happens on similar graphs for the case where $r = \kappa$. New graphs will only be drawn in this case if the fundamental shape is different than what was achieved with the $r \neq \kappa$ graphs. For all of these graphs, the curve drawn will be the right hand side of (5.2) or (5.3); the region where the condition will be met will thus be any points

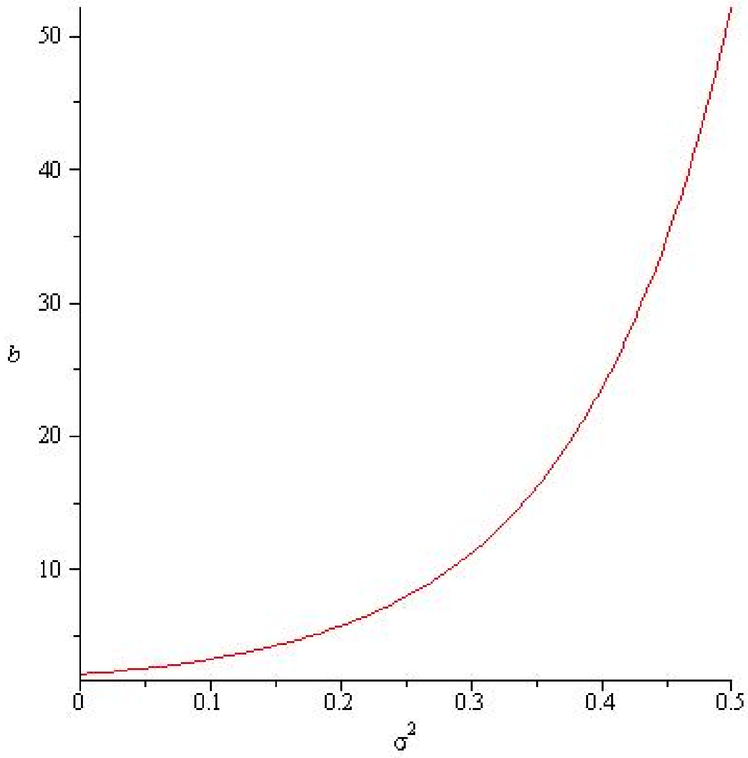

Figure 5.2: Sufficient growth condition for annuals with respect to volatility, σ^2

above the curve.

The first parameter we will consider is σ. Figure 5.2 compares b with σ^2, fixing $r = 0.0225$, $\kappa = 0.05$, and $T = 20$. Thus, according to this graph, it appears the reproductive utility needed to ensure at least a 50% chance of growth increases as σ increases. This makes sense since, if σ increases, then the volatility of the environment increases, meaning that large losses (large gains as well) of biomass become more likely to occur. As a result, the utility of the seeds should increase enough to help offset the potential higher losses during the season.

Remark: A rigorous proof of the properties of Figure 5.1 discussed (as well as those of the following graphs) is given in the next subsection.

Note that the graph for the case $r = \kappa$ will look the same (in shape) because the

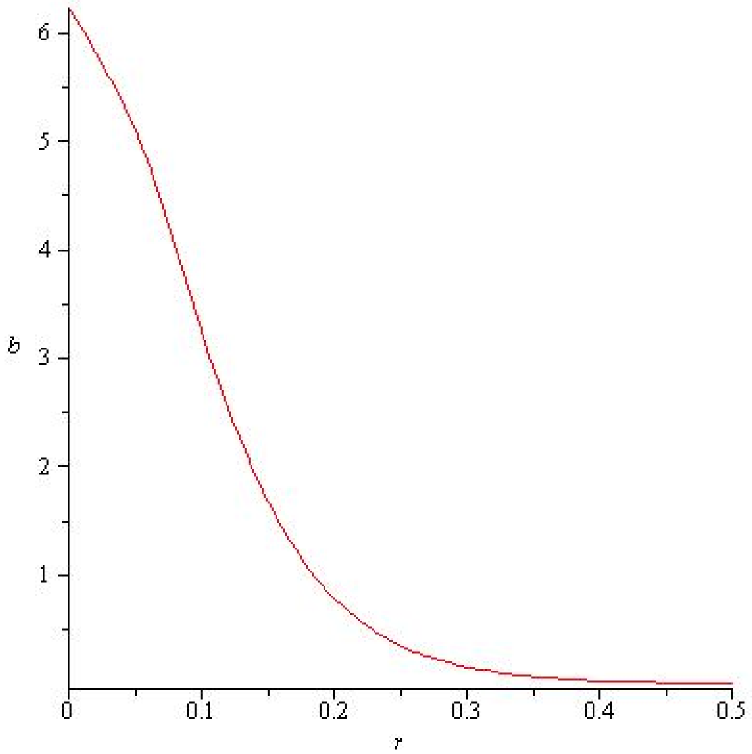

Figure 5.3: Sufficient growth condition for annuals with respect to growth rate, r

piece in (5.2) and (5.3) that is dependent on σ, $f(r, \sigma, T)$, is exactly the same as when $r \neq \kappa$. Hence, we will omit the graph in this case.

The next parameter we will consider is r. Figure 5.3 compares b with r, fixing $\kappa = 0.05$, $\sigma^2 = 0.2$, and $T = 20$. So, according to this graph, as the growth rate increases, the requirement for reproductive utility decreases. This certainly makes sense since, when r increases, we expect that the amount of new biomass produced in each instant will increase as well. Also, when r increases, as shown before, d_A increases (in many cases), so the plants will then usually wait a longer time before reproduction begins. Thus, for a large growth rate, it is expected that much more biomass will be available when reproduction begins, and hence less reproductive utility should be needed.

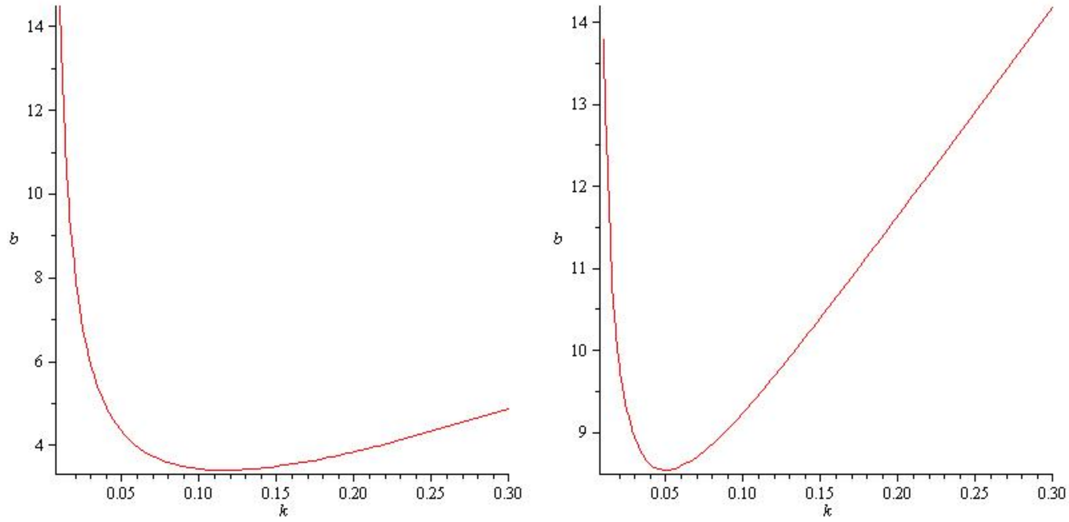

Figure 5.4: Sufficient growth condition for annuals with respect to maximum reproduction proportion, κ ($r = 0.03$, $\sigma^2 = 0.2$, $T = 10$ on the left; $r = 0.05$, $\sigma^2 = 0.2$, $T = 30$ on the right)

The next parameter we will consider is κ. Figure 5.4 compares b with κ on two graphs. The graph on the left fixes $r = 0.03$, $\sigma^2 = 0.2$, and $T = 10$, and the graph on the right fixes $r = 0.05$, $\sigma^2 = 0.2$, and $T = 30$. On each of these graphs, we note that the overall behavior is the same: for very small values of κ, the utility requirement is very large. As κ increases, however, this is followed by a sharp decrease in the requirement until a minimum is reached, after which the requirement begins increasing again, but at a slower rate than the initial decrease.

Biologically, it certainly makes sense to have a very high reproductive utility requirement when κ is very close to 0 because, if almost nothing can be put into reproduction at any instant, the small amount that can be put in needs to have a high utility in order to ensure growth for the next season since this is the only way annuals can carry biomass into the next season. On the other hand, increasing κ too much results in "self-cannibalization" of the resources; that is, the plants begin to use up any growth they may experience and more for reproduction. Because of

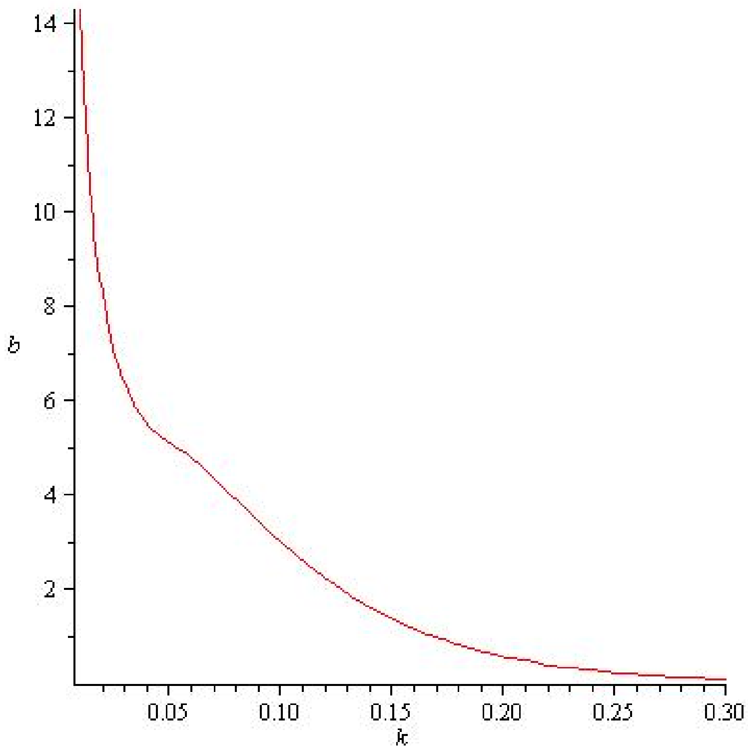

Figure 5.5: Sufficient growth condition for annuals with respect to growth rate = maximum reproduction proportion, $r = \kappa$

that, if the season length is fixed, then the plants not only will, in many cases, wait longer to reproduce as discussed previously, which increases their risk of decay, but they most likely cannot sufficiently replenish themselves when reproduction actually begins. These two facts could result in less biomass being used for reproduction, thus requiring a higher utility for likely growth next season.

Of course, one issue that should be addressed is where that "minimum" utility requirement actually occurs. The short answer is that it "occurs" at $\kappa = r$ when $T \geq 1/r$ (this point is not defined on this graph) and occurs at some $\kappa > r$ when $T < 1/r$.

But, if we consider the case where $r = \kappa$, this type of behavior doesn't quite occur. Figure 5.5 illustrates this, fixing $\sigma^2 = 0.2$ and $T = 20$. Note that this graph

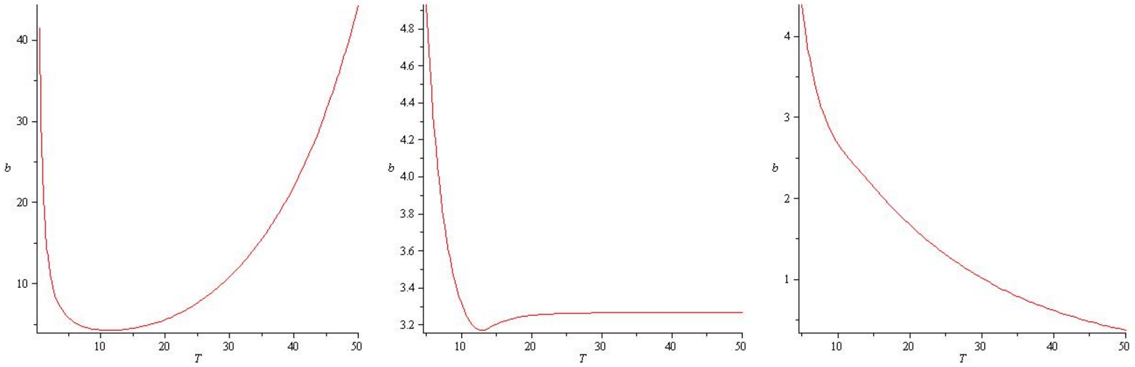

Figure 5.6: Sufficient growth condition for annuals with respect to season length, T ($r = 0.03$ for left graph, $r = 0.1$ for middle graph, $r = 0.15$ for right graph)

does show the same behavior as Figure 5.4 when κ is very close to 0, but, unlike when $r \neq \kappa$, the utility requirement decreases whenever κ increases for all values of κ, eventually approaching 0. This is because, in this case, notice that κ plays the role of both the growth rate and the reproduction rate, and so, when κ is small here, virtually no growth and no reproduction are taking place, so there should be a large utility requirement. However, as κ increases, no "self-cannibalization" occurs since the growth and reproduction rates are the same, so more biomass is expected to be available and devoted to reproduction when reproduction begins (starting time for reproduction will, in most cases, be delayed as κ increases), and hence the utility requirement can be eased.

Our final parameter to consider is T. This is probably the most interesting parameter of all since three distinct types of behavior can occur. Figure 5.6 illustrates this by fixing $\kappa = 0.05$ and $\sigma^2 = 0.2$ for all three graphs, but fixing different values of r for each graph; specifically, $r = 0.03$ on the left, $r = 0.1$ in the middle, and $r = 0.15$ on the right. In all 3 scenarios, we notice that, when the season is very short, the utility requirement is very large. However, as the season length increases, one of three long-term behaviors may occur. In the first scenario ($r = 0.03$), note that, as T increases, the utility requirement on initially decreases, but, after hitting a minimum, the requirement then increases and does so from then on. In the second scenario ($r = 0.1$), we note that, instead of the utility requirement increasing after hitting a minimum unboundedly, it approaches a finite limit. However, in the third scenario ($r = 0.15$), the utility requirement initially follows the same behavior as in the first two scenarios, but then begins to decrease to 0. Since there is markedly different behavior for increasing T in each scenario, it is important to determine under what conditions each will occur.

Since both κ and σ^2 were fixed when drawing these graphs, it appears that r makes the difference. Note that, in the first scenario, $r < (1/2)\sigma^2$, in the second, $r = (1/2)\sigma^2$, and, in the third, $r > (1/2)\sigma^2$. Recall the random variable governing single-season dynamics is

$$Y_t = \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \int_0^t \kappa H(s - d_A)ds + \sigma B_t\right),$$

where $d_A = T - \frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)$. Since $\exp((r - (1/2)\sigma^2)t)$ shows up as a deterministic piece in Y_t, based on this and the prior observations, it makes sense that the crtical value would be $r = (1/2)\sigma^2$.

Biologically, we can explain what's going on by considering the single-season dynamics. Fixing all parameters besides T gives us $d_A = T - C$, where $C > 0$ is a constant determined by r, κ, if $d_A > 0$. This means that, when T is increased, the amount of absolute time spent reproducing never changes (except when $C \geq T$ since, in this case, $d_A = 0$). This extra time during the season is then used solely for growth and maintenance (except when $C \geq T$), meaning that the plants are playing for a longer time against the risky environment.

Because $E[dB_t] = 0$ for any t, then, during the time when no reproduction takes place, we turn to $(r - (1/2)\sigma^2)$ to determine if we expect growth during any given instant or not. If $r < (1/2)\sigma^2$, then we expect decay, meaning that there is more reliance on a “good” environment in order to experience growth. Because of this, as T increases, there is an expectation of more decay before reproduction begins, and hence the reproductive utility should be high enough to offset the expected loss to ensure (most of the time) season-to-season growth. This is why we see, as T gets larger, that the requirement for b increases in this case.

If $r > (1/2)\sigma^2$ on the other hand, then we expect growth during any given instant, meaning that, if there is more time during the season to devote to growth and maintenance, we would expect a greater amount of biomass to convert to seeds when reproduction time begins. Hence, there would not need to be as much of a reliance on the utility of those seeds to have season-to-season growth, so this is why, as T gets larger, we see the requirement for b decreasing.

However, for lower values of T, increasing T decreases the requirement on b in all three scenarios. This is due to the fact that, when T is sufficiently small, season-long reproduction takes place. This continues until $T = C$, after which any additional time gets devoted to growth and maintenance. So, initially, additional time adds to reproduction, not growth/maintenance. And, as a result, more biomass can then be poured into reproduction (a short season lessens the effects of the volatility on the population as well), which means that the utility requirement can be lowered.

The same behavior is observed in the case when $r = \kappa$, so we will not draw a graph for this case.

5.2.3 Analytic Properties of Sufficient Growth Condition

We now mathematically prove some of the claims made in the previous section based on graphs as well as biological intuition. Specifically, we are looking at what b, the reproductive utility, should be in order to guarantee that the sufficient growth condition, (5.2) or (5.3), holds. If it does, then there will be at least a 50% chance for growth over a sufficiently large number of seasons.

We begin by looking at the asymptotic behavior of the utility requirement with respect to σ^2. To do so, we only need to look at $f(r, \sigma, T)$ since this is the only part of either (5.2) or (5.3) that depends on σ. Recall that

$$f(r, \sigma, T) = \left(\frac{1}{r(2r + \sigma^2)} - \frac{\exp(rT)}{r(r + \sigma^2)} + \frac{\exp((2r + \sigma^2)T)}{(2r + \sigma^2)(r + \sigma^2)} \right)^{1/2}.$$

So, the first two terms under the square root clearly approach 0 as σ^2 becomes very large, and the third term grows like $\exp((2r + \sigma^2)T)$ as σ^2 becomes very large. Thus, $\lim_{\sigma^2 \to \infty} f(r, \sigma, T) = \infty$, and so the utility requirement should be increasing exponentially for large σ. This confirms our prediction that the utility requirement increases unboundedly when discussing Figure 5.2.

Next, we look at the asymptotic behavior of the utility requirement with respect to r. Specifically, noting that

$$\lim_{r \to \infty} \frac{1}{r - \kappa} \ln \left(\frac{r}{\kappa} \right) = 0,$$

then it follows that, as $r \to \infty$, $d_A \to T > 0$, meaning that we want to find:

$$\begin{aligned}
&\lim_{r\to\infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT-\kappa(T-d_A)) - \exp(rd_A))^{-2} \cdot f(r,\sigma,T) \\
&= \lim_{r\to\infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}\left(\exp\left(rT-\kappa\left(\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right)\right)\right. \\
&\qquad\qquad\left. -\exp\left(r\left(T-\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right)\right)\right)^{-2} \cdot f(r,T,\sigma^2).
\end{aligned}$$

Noting, using l'Hospital's Rule,

$$\begin{aligned}
\lim_{r\to\infty} \frac{r}{r-\kappa}\ln\left(\frac{r}{\kappa}\right) &= \lim_{r\to\infty} \ln(r) - \ln(\kappa) + 1 \\
&= \infty,
\end{aligned}$$

then

$$\begin{aligned}
&\lim_{r\to\infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}\left(\exp\left(rT-\kappa\left(\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right)\right)\right. \\
&\qquad\qquad\left. -\exp\left(r\left(T-\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right)\right)\right)^{-2} \cdot f(r,T,\sigma^2) \\
&= \lim_{r\to\infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}\left(\exp\left(-\frac{\kappa}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right) - \exp\left(-\frac{r}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right)\right)^{-2} \\
&\qquad \cdot \exp(-2rT)\left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(rT)}{r(r+\sigma^2)} + \frac{\exp((2r+\sigma^2)T}{(2r+\sigma^2)(r+\sigma^2)}\right)^{1/2} \\
&= \lim_{r\to\infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa} \cdot \left(\exp\left(-\frac{\kappa}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right) - \exp\left(-\frac{r}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)\right)\right)^{-2} \\
&\qquad \cdot \left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(-3rT)}{r(r+\sigma^2)} + \frac{\exp((-2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)^{1/2} \\
&= 0
\end{aligned}$$

since the quantity taken to the 1/2 power decays according to $\exp(-3rT)$ as $r \to \infty$, and the other factor grows according to $(r-\kappa)^2$ (the quantity raised to the -2 power approaches 1 by the given facts above). But, $\exp(-(3/2)rT)$ decays much faster than $(r-\kappa)^2$ grows, and hence the limit is 0 and is approached exponentially as r becomes very large. This confirms our prediction that the utility requirement decreases to 0 as r becomes very large when looking at Figure 5.3.

Next, we consider the asymptotic behavior of the utility requirement with respect to κ. We'll begin by looking at the case where $r \neq \kappa$. Noting that

$$\lim_{\kappa \to 0^+} \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right) = \infty,$$

then, as $\kappa \to 0^+$, $d_A \to 0$, and hence we want to compute

$$\lim_{\kappa \to 0^+} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT - \kappa T))^{-2}.$$

This is the only part of (5.2) that is dependent on κ; thus,

$$\begin{aligned} &\lim_{\kappa \to 0^+} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT - \kappa T) - 1)^{-2} \\ &= \lim_{\kappa \to 0^+} \sqrt{2}\left(\frac{r}{\sqrt{\kappa}} - \sqrt{\kappa}\right)^2 (\exp(rT - \kappa T) - 1)^{-2} \\ &= \infty \end{aligned}$$

since $\frac{r}{\sqrt{\kappa}} \to \infty$ as $\kappa \to 0^+$, and every other quantity involved approaches a finite limit. So, as κ becomes very small, we note that the sufficient utility requirement increases like $f(x) = x^{-1/2}$, which we can observe in Figure 5.4.

Next, we note that there is a "minimum" utility requirement reached on the graphs in Figures 5.4 and 5.5; we would like to get a better idea of the location of that minimum. To do so, recalling that

$$\lim_{\kappa \to r} \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right) = \frac{1}{r},$$

then the relevant branch of (5.2) as $\kappa \to r$ is determined by whether $T \leq 1/r$ (in which case, the branch where $d_A = 0$ is relevant) or $T > 1/r$ (in which case, the branch where $d_A > 0$ is relevant). In the latter case, we note that, using Maple, we find that

$$\lim_{\kappa \to r} \frac{\partial}{\partial \kappa} \left(\frac{\sqrt{2}(r-\kappa)^2}{\kappa} \exp(-2rT) \left(\left(\frac{r}{\kappa}\right)^{-\frac{\kappa}{r-\kappa}} - \left(\frac{r}{\kappa}\right)^{-\frac{r}{r-\kappa}} \right)^{-2} \right) = 0$$

and

$$\lim_{\kappa \to r} \frac{\partial^2}{\partial \kappa^2} \left(\frac{\sqrt{2}(r-\kappa)^2}{\kappa} \exp(-2rT) \left(\left(\frac{r}{\kappa}\right)^{-\frac{\kappa}{r-\kappa}} - \left(\frac{r}{\kappa}\right)^{-\frac{r}{r-\kappa}} \right)^{-2} \right) = \frac{\sqrt{2} \cdot \exp(2)}{3r \cdot \exp(2rT)}.$$

Hence, if $T \geq 1/r$, $r = \kappa$ represents a “local minimum” (we use quotes since the point where $r = \kappa$ is undefined here, which is why we had to take limits above) for the utility requirement.

However, if $T < 1/r$, then the above result does not hold. In fact, using Maple, we find that

$$\lim_{\kappa \to r} \frac{\partial}{\partial \kappa} \left(\frac{\sqrt{2}(r-\kappa)^2}{\kappa} (\exp(rT - \kappa T))^{-2} \right) = \sqrt{2} \left(\frac{rT-1}{r^2 T^2} \right).$$

But, since $T < 1/r$, then this quantity is negative. Thus, the utility requirement is still decreasing near this point. Next, we note that

$$\lim_{\kappa \to \infty} T - \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right) = T.$$

Thus, as $\kappa \to \infty$, $d_A \to T > 0$. So, to analyze what happens as $\kappa \to \infty$, we want to compute

$$\lim_{\kappa \to \infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa} \left(\exp\left(rT - \kappa(T-d_A)\right) - \exp\left(rd_A\right)\right)^{-2}.$$

Noting, using l'Hospital's Rule,

$$\begin{aligned} \lim_{\kappa \to \infty} \frac{\kappa}{r-\kappa} \ln\left(\frac{r}{\kappa}\right) &= \lim_{\kappa \to \infty} -\ln(r) + \ln(\kappa) + 1 \\ &= \infty, \end{aligned}$$

then

$$\lim_{\kappa \to \infty} \frac{\sqrt{2}(r-\kappa)^2}{\kappa} \left(\exp\left(rT - \kappa(T-d_A)\right) - \exp\left(rd_A\right)\right)^{-2} = \infty$$

since the quantity being raised to the -2 power approaches 1 by the above facts, and the quantity outside of it increases like κ. So, the utility requirement increases linearly for large values of κ. Also, because we've shown that, when $T < 1/r$, the utility requirement is decreasing at the "point" $r = \kappa$, then it must follow, by continuity, that there is some minimum utility requirement for some $\kappa^* > r$.

Next, we look at the case where $r = \kappa$. Here, since $\lim_{\kappa \to 0^+} T - \frac{1}{\kappa} = -\infty$, the utility requirement as $\kappa \to 0^+$ is given by

$$\lim_{\kappa \to 0^+} \frac{\sqrt{2}}{\kappa T^2} \cdot f(\kappa, T, \sigma) = \infty$$

since we can rewrite $f(\kappa, T, \sigma)$ as

$$f(\kappa, T, \sigma) = \left(\frac{(\kappa + \sigma^2) - (2\kappa + \sigma^2)\exp(\kappa T) + \kappa \cdot \exp((2\kappa + \sigma^2)T)}{\kappa(\kappa + \sigma^2)(2\kappa + \sigma^2)}\right)^{1/2}.$$

Then, by l'Hospital's Rule, we find that, as $\kappa \to 0^+$, this quantity approaches

$$\left(\frac{-1-\sigma^2 T+\exp(\sigma^2 T)}{\sigma^4}\right)^{1/2}.$$

Thus, since $1/\kappa \to \infty$ as $\kappa \to 0^+$, we see that, indeed, the utility requirement approaches infinity as $\kappa \to 0^+$ and does so like $f(x) = x^{-1}$. We can observe this on the graph in Figure 5.5.

Also, the behavior as $\kappa \to \infty$ is given by

$$\begin{aligned}
&\lim_{\kappa\to\infty} \kappa\sqrt{2}\cdot\exp(2-2\kappa T)\cdot f(\kappa,T,\sigma)\\
&=\lim_{\kappa\to\infty} \sqrt{2}\cdot\exp(2)\\
&\qquad\cdot\left(\frac{\kappa\cdot\exp(-4\kappa T)}{2\kappa+\sigma^2}-\frac{\kappa\cdot\exp(-3\kappa T)}{(\kappa+\sigma^2)}+\frac{\kappa^2\cdot\exp((-2\kappa+\sigma^2)T)}{(2\kappa+\sigma^2)(\kappa+\sigma^2)}\right)^{1/2}\\
&=0
\end{aligned}$$

since, as $\kappa \to \infty$, $T - 1/\kappa \to T > 0$, so $d_A^* > 0$. So, as κ becomes very large, the utility requirement decays exponentially to 0 (like $\exp(-2\kappa T)$).

Remark: Of course, by definition, $\kappa < 1 + r$, so it is not practical to consider very large values of κ. But, we can at least confirm mathematically that the utility requirement should increase without bound for large values of κ when $r \neq \kappa$ and should decrease to 0 for large values of κ when $r = \kappa$, which is what we observed on the graphs in Figures 5.4 and 5.5.

Finally, we consider what happens with the utility requirement when changing the parameter T. For this analysis, we assume $r \neq \kappa$ since the analysis for $r = \kappa$ works exactly the same way and produces the same overall results. Thus, for brevity, we will omit this case. So, we first note

$$\lim_{T \to 0^+} \frac{\sqrt{2}(r-\kappa)^2}{\kappa}(\exp(rT-\kappa T)-1)^{-2} \cdot f(r,T,\sigma) = \infty.$$

The branch of (5.2) where $d_A = 0$ is used here because, as discussed previously, $\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right)$ is strictly positive whenever $r \neq \kappa$. The limit is computed by noting that, clearly, $\lim_{T\to 0^+} f(r,T,\sigma)$ is finite, and $\exp(rT-\kappa T) \to 1$. Hence, as T becomes very small, the utility requirement will increase exponentially. This can be observed on all of the graphs in Figure 5.6.

However, as T gets very large, the behavior is a little more tricky to figure out. As the graphs in Figure 5.6 indicate, we should test values of r around $(1/2)\sigma^2$. So, let $\delta > 0$ be given. Then, plugging in $r = (1/2)\sigma^2 - \delta$ (in this case, also assume that $\delta < (1/2)\sigma^2$ because, practically, we expect $r > 0$ for a viable species), and defining

$$\bar{d_A} = \frac{1}{(1/2)\sigma^2 - \delta - \kappa}\ln\left(\frac{(1/2)\sigma^2 - \delta}{\kappa}\right),$$

we note the following (use the branch where $d_A > 0$ here since $\bar{d_A}$ remains constant with respect to T):

$$\begin{aligned}
&\lim_{T\to\infty} \frac{\sqrt{2}((1/2)\sigma^2-\delta-\kappa)^2}{\kappa} \\
&\qquad \cdot \big(\exp(((1/2)\sigma^2-\delta)T-\kappa(\bar{d_A}))-\exp(((1/2)\sigma^2-\delta)(T-\bar{d_A}))\big)^{-2} \\
&\qquad \cdot \bigg(\frac{1}{((1/2)\sigma^2-\delta)(2\sigma^2-2\delta)}-\frac{\exp(((1/2)\sigma^2-\delta)T)}{((1/2)\sigma^2-\delta)((3/2)\sigma^2)-\delta} \\
&\qquad\quad +\frac{\exp((2\sigma^2-2\delta)T)}{(2\sigma^2-2\delta)((3/2)\sigma^2-\delta)}\bigg)^{1/2} \\
&=\lim_{T\to\infty} \frac{\sqrt{2}((1/2)\sigma^2-\delta-\kappa)^2}{\kappa}\big(\exp(-\kappa(\bar{d_A}))-\exp(-((1/2)\sigma^2-\delta)\bar{d_A})\big)^{-2} \\
&\qquad \cdot \bigg(\frac{\exp(-4((1/2)\sigma^2-\delta)T)}{((1/2)\sigma^2-\delta)(2\sigma^2-2\delta)}-\frac{\exp(-3((1/2)\sigma^2-\delta)T)}{((1/2)\sigma^2-\delta)((3/2)\sigma^2)-\delta} \\
&\qquad\quad +\frac{\exp(2\delta T)}{(2\sigma^2-2\delta)((3/2)\sigma^2-\delta)}\bigg)^{1/2} \\
&=\infty
\end{aligned}$$

since, by assumption, $(1/2)\sigma^2-\delta$ is strictly positive, meaning that, looking at the quantity raised to the $1/2$ power, the first two terms go to 0, but the last one goes to infinity, meaning the limit must equal infinity, and the utility requirement increases exponentially (like $\exp(\delta T)$).

If we assume that $r=(1/2)\sigma^2+\delta$ (we only need $\delta>0$ here), then, noting that the only changes in the above computations are flipping the δ's to $-\delta$'s, then we have that the utility requirement approaches 0 as $T\to\infty$. This is because the last term in the quantity being raised to the $1/2$ power now goes to 0 since it decays like $\exp(-2\delta T)$, and so the utility requirement decreases exponentially in this case to 0.

Finally, if we assume that $r=(1/2)\sigma^2$, setting $\delta=0$ in the above computations gives us that, as $T\to\infty$, the utility requirement approaches

$$\frac{\sqrt{2}((1/2)\sigma^2-\kappa)^2}{\kappa}\big(\exp(-\kappa(\bar{d_A}))-\exp(-((1/2)\sigma^2)\bar{d_A})\big)^{-2}\left(\frac{1}{(2\sigma^2)((3/2)\sigma^2)}\right)^{1/2},$$

where

$$\bar{d_A} = \frac{1}{(1/2)\sigma^2 - \kappa} \ln\left(\frac{(1/2)\sigma^2}{\kappa}\right).$$

These computations confirm all of our observations when discussing Figure 5.6.

Remark: For reference, if $\kappa = (1/2)\sigma^2$ in the case $r = \kappa$, then, as $T \to \infty$, the utility requirement approaches

$$\frac{\sqrt{2}\sigma^2}{2} \cdot \exp(2) \left(\frac{1}{(2\sigma^2)((3/2)\sigma^2)}\right)^{1/2}.$$

5.3 Case 3: $a > 0$, $b/a > 1$

5.3.1 Derivation of a Sufficient Growth Condition

The final case concerns perennials whose optimal strategy is to reproduce at some point during the season. The analysis for this case will proceed almost exactly like Case 2 in that we will derive an upper bound on the variance of $X_1 \cdots X_n$, where, for all $i = 1, 2, \ldots$,

$$\begin{aligned} X_i = a \cdot \exp&\left(\left(r - \frac{1}{2}\sigma^2\right)T + \kappa(T - d_P) + \sigma B_T\right) \\ &+ b\kappa \int_{d_P}^{T} \exp\left(\left(r - \frac{1}{2}\sigma^2\right)s - \kappa(s - d_P) + \sigma B_s\right) ds, \end{aligned}$$

where

$$d_P = \begin{cases} T - \frac{1}{r-\kappa} \ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right) & r \neq \kappa \\ T - \frac{b-a}{b\kappa} & r = \kappa \end{cases}.$$

Should either expression be negative, then we set $d_P = 0$; also, for distinction, we set $d_P^* = T - \frac{b-a}{b\kappa}$.

Recalling that, by Remark 2 after Theorem 4.6,

$$E[X_n] = \begin{cases} \left(a + \frac{b\kappa}{r-\kappa}\right) \exp(rT - \kappa(T - d_P)) - \frac{b\kappa}{r-\kappa} \exp(r d_P) & r \neq \kappa \\ b \cdot \exp(\kappa d_P^*) & r = \kappa \end{cases},$$

we now attempt to find an upper bound on the variance as follows: First, by definition, for any two random variables X, Y,

$$\begin{aligned} \mathrm{Var}(X+Y) &= E[(X+Y)^2] - E[X+Y]^2 \\ &= E[X^2] + 2E[XY] + E[Y^2] - E[X+Y]^2. \end{aligned}$$

In this case, note that we can write $X_n = Z_1 + Z_2$ for any n, where:

$$\begin{aligned} Z_1 &= a \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right) T + \kappa(T - d_P) + \sigma B_T\right) \\ Z_2 &= b\kappa \int_{d_P}^{T} \exp\left(\left(r - \frac{1}{2}\sigma^2\right) s - \kappa(s - d_P) + \sigma B_s\right) ds. \end{aligned}$$

Z_1 is the random variable we analyzed in Case 1, and Z_2 is the random variable we analyzed in Case 2. Hence, most of the work in finding an upper bound on $\mathrm{Var}(X_n)$ has already been done because we know what $E[(Z_1)^2]$ and $E[X_1]^2 = E[Z_1 + Z_2]^2$ are, and we have an upper bound on $E[(Z_2)^2]$. All that remains is to find an upper bound on $E[Z_1 \cdot Z_2]$. To do this, we again turn to Yor ([28, p. 521]), which gives us the following formula:

Lemma 5.2: For any $\lambda \geq 0$, $\alpha \geq 0$, and $n = 1, 2, \ldots$,

$$E\left[\exp\left(\lambda(B_T + \alpha T)\right) \cdot \left(\int_0^T \exp(B_t + \alpha t)dt\right)^n\right]$$
$$= E\left[n! \sum_{j=0}^{n} c_j^{(\alpha+\lambda)} \cdot \exp(j(B_T + \alpha T)) \cdot \exp(\lambda(B_T + \alpha T))\right],$$

where

$$c_j^{(x)} = \prod_{k=0, k \neq j}^{n} \left(\frac{(x+j)^2}{2} - \frac{(x+k)^2}{2}\right)^{-1}.$$

Proof: A proof of this can be found in [28, p. 521].

Comparing this with Lemma 5.1, we notice a key difference in their hypotheses and the form of the final results: the parameters λ, α are required to be nonnegative in Lemma 5.2, which was not the case in Lemma 5.1. With this in mind, we first note that, for any given path of B_t, we have the following:

$$\exp\left(\left(r - \frac{1}{2}\sigma^2\right)T - \kappa(T - d_P) + \sigma B_T\right)$$
$$\cdot \int_{d_P}^{T} \exp\left(\left(r - \frac{1}{2}\sigma^2\right)t - \kappa(t - d_P) + \sigma B_t\right) dt$$
$$\leq \exp(rT + \sigma B_T) \cdot \int_0^T \exp(rt + \sigma B_t)dt. \tag{5.4}$$

We used a similar inequality in Case 2 to find an upper bound for the variance, but here, to get a universal upper bound, we drop the $-(1/2)\sigma^2 T$ in the exponents since it is possible for $r - (1/2)\sigma^2$ to be negative, which would violate the hypotheses of the lemma.

Another key difference in the statement of Lemma 5.2 from Lemma 5.1 is that, in the integrand, the B_t in the exponent has no scalar multiple. So, we will need to make an appropriate transformation to ensure that we still have a Standard Brownian

Motion. Specifically, we note that, if B_t is a Standard Brownian Motion, then so is $\frac{1}{c}B_{c^2t}$ for any $c \neq 0$ (see, for example, [22, p. 18]). Based on this, we have the following:

$$\begin{aligned}
&E\left[a \cdot \exp(rT + \sigma B_T) \cdot b\kappa \int_0^T \exp(rt + \sigma B_t)dt\right] \\
&= ab\kappa \cdot E\left[\exp(rT + B_{\sigma^2 T}) \cdot \int_0^T \exp(rt + B_{\sigma^2 t})dt\right] \\
&= ab\kappa \cdot E\left[\exp((r/\sigma^2)T\sigma^2 + B_{\sigma^2 T}) \cdot \frac{1}{\sigma^2}\int_0^{\sigma^2 T} \exp((r/\sigma^2)u + B_u)du\right]
\end{aligned}$$

after making the substitution $u = \sigma^2 t$. Now, by Lemma 5.2, we compute this as follows, taking $\lambda = 1$ and $\alpha = r/\sigma^2$:

$$\begin{aligned}
&\frac{ab\kappa}{\sigma^2}E\left[\exp((r/\sigma^2)T\sigma^2 + B_{\sigma^2 T}) \cdot \int_0^{\sigma^2 T} \exp((r/\sigma^2)u + B_u)du\right] \\
&= \frac{ab\kappa}{\sigma^2}E\Bigg[\exp((r/\sigma^2)T\sigma^2 + B_{\sigma^2 T})\left(\frac{((r/\sigma^2)+1)^2}{2} - \frac{((r/\sigma^2)+2)^2}{2}\right)^{-1} \\
&\qquad \cdot \left(1 - \exp((r/\sigma^2)T\sigma^2 + B_{\sigma^2 T})\right)\Bigg] \\
&= \frac{ab\kappa}{\sigma^2}E\left[\frac{2\sigma^2}{2r + 3\sigma^2}\left(\exp(2rT + 2B_{\sigma^2 T}) - \exp(rT + B_{\sigma^2 T})\right)\right] \\
&= \frac{2ab\kappa}{2r + 3\sigma^2}\left(\exp((2r + 2\sigma^2)T) - \exp((r + (1/2)\sigma^2)T)\right).
\end{aligned}$$

Remark: As mentioned previously, this is not a tight upper bound, as the bound can be made tighter when $r - (1/2)\sigma^2$ is nonnegative. In that case, following the same argument as above, but taking $\alpha = r/\sigma^2 - 1/2$, one can obtain the upper bound of

$$\frac{ab\kappa}{r + \sigma^2}\left(\exp((2r + \sigma^2)T) - \exp(rT)\right).$$

For the remainder of this section, we will stick with the more universal upper bound derived previously, even if $r - (1/2)\sigma^2$ is nonnegative. In the following sections, we will only use this tighter bound if it produces a significantly different result than the universal upper bound.

With all of this information, we can now establish an upper bound on $\mathrm{Var}(X_n) = \mathrm{Var}(Z_1 + Z_2)$ as follows:

$$\begin{aligned}
\mathrm{Var}(X_n) \leq E[(Z_1)^2] &+ 2E\left[a \cdot \exp(rT + \sigma B_T) \cdot b\kappa \int_0^T \exp(rt + \sigma B_t)dt\right] \\
&+ E[(Z_2^*)^2] - (E[X_1])^2 \\
= a^2 &\cdot \exp(2(rT - \kappa(T - d_P)) + \sigma^2 T) \\
&+ \frac{4ab\kappa}{2r + 3\sigma^2}\big(\exp((2r + 2\sigma^2)T) - \exp((r + (1/2)\sigma^2)T)\big) \\
&+ 2b^2\kappa^2\left(\frac{1}{r(2r + \sigma^2)} - \frac{\exp(rT)}{r(r + \sigma^2)} + \frac{\exp((2r + \sigma^2)T)}{(2r + \sigma^2)(r + \sigma^2)}\right) \\
&- \left(\left(a + \frac{b\kappa}{r - \kappa}\right)\exp(rT - \kappa(T - d_P)) - \frac{b\kappa}{r - \kappa}\exp(rd_P)\right)^2.
\end{aligned}$$

Next, as in the annuals case, since we are assuming n is sufficiently large, we can get estimates μ^* and $(\nu^*)^2$ on the mean and variance μ and ν^2, respectively, of the corresponding approximate underlying normal distribution to $X_1 \cdots X_n$ as follows:

$$
\begin{aligned}
\nu^2 &= \ln\left(1 + \frac{\operatorname{Var}(X_1 \cdots X_n)}{E[X_1 \cdots X_n]^2}\right) \\
&\leq \ln\left(\frac{E[(X_n^*)^2]^n}{E[X_n]^{2n}}\right) \\
&= (\nu^*)^2 \\
(\nu^*)^2 &= n \ln \big(a^2 \cdot \exp(2(rT - \kappa(T - d_P)) + \sigma^2 T) \\
&\qquad\qquad + \frac{4ab\kappa}{2r + 3\sigma^2}(\exp((2r + 2\sigma^2)T) - \exp((r + (1/2)\sigma^2)T)) \\
&\qquad\qquad + 2b^2\kappa^2 \left(\frac{1}{r(2r + \sigma^2)} - \frac{\exp(rT)}{r(r + \sigma^2)} + \frac{\exp((2r + \sigma^2)T)}{(2r + \sigma^2)(r + \sigma^2)}\right)\Big) \\
&\quad + n \ln\left(\left(\left(a + \frac{b\kappa}{r - \kappa}\right)\exp(rT - \kappa(T - d_P)) - \frac{b\kappa}{r - \kappa}\exp(rd_P)\right)^{-2}\right) \\
\mu &= \ln(E[X_1 \cdots X_n]) - \frac{1}{2}\nu^2 \\
&\geq \ln(E[X_n]^n) - \frac{1}{2}(\nu^*)^2 \\
&= \mu^* \\
\mu^* &= n \ln\left[\left(\left(a + \frac{b\kappa}{r - \kappa}\right)\exp(rT - \kappa(T - d_P)) - \frac{b\kappa}{r - \kappa}\exp(rd_P)\right)^2\right] \\
&\quad + n \ln\Big[\big(a^2 \cdot \exp(2(rT - \kappa(T - d_P)) + \sigma^2 T) \\
&\qquad\qquad + \frac{4ab\kappa}{2r + 3\sigma^2}\big(\exp((2r + 2\sigma^2)T) - \exp((r + (1/2)\sigma^2)T)\big) \\
&\qquad\qquad + 2b^2\kappa^2 \left(\frac{1}{r(2r + \sigma^2)} - \frac{\exp(rT)}{r(r + \sigma^2)} + \frac{\exp((2r + \sigma^2)T)}{(2r + \sigma^2)(r + \sigma^2)}\right)\bigg)^{-1/2}\Bigg].
\end{aligned}
$$

Thus, if we want to guarantee long-term population growth for these perennials at least 50% of the time, we want $\mu^* > 0$, or, equivalently, $\exp(\mu^*) > 1$; for this to happen, we need

$$\begin{aligned}
&\left(a \cdot \exp(rT - \kappa(T - d_P)) + \frac{b\kappa}{r-\kappa}\left(\exp(rT - \kappa(T - d_P)) - \exp(rd_P)\right)\right)^2 \\
&\cdot \big[a^2 \cdot \exp(2(rT - \kappa(T - d_P)) + \sigma^2 T) \\
&\quad + \frac{4ab\kappa}{2r + 3\sigma^2}\big(\exp((2r + 2\sigma^2)T) - \exp((r + (1/2)\sigma^2)T)\big) \\
&\quad + 2b^2\kappa^2\left(\frac{1}{r(2r+\sigma^2)} - \frac{\exp(rT)}{r(r+\sigma^2)} + \frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right)\big]^{-1/2} > 1. \qquad (5.5)
\end{aligned}$$

Unfortunately, this inequality cannot be solved easily for b (or any other parameter, for that matter), unlike the inequality from the annuals case. This means we will have to analyze this inequality as it is given above.

We also note that, if $r = \kappa$, then the only change in the above sufficient growth condition is replacing the quantity being squared, which is $E[X_n]$, with the corresponding value when $r = \kappa$, and replacing all r's with κ's elsewhere (resulting in using d_P^* as opposed to d_P). This gives the sufficient condition for growth at least 50% of the time of:

$$\begin{aligned}
&((a + b\kappa(T - d_P^*)) \cdot \exp(\kappa d_P^*))^2 \\
&\cdot \big[a^2 \cdot \exp(2\kappa d_P^* + \sigma^2 T) \\
&\quad + \frac{4ab\kappa}{2\kappa + 3\sigma^2}\big(\exp((2\kappa + 2\sigma^2)T) - \exp((\kappa + (1/2)\sigma^2)T)\big) \\
&\quad + 2b^2\kappa^2\left(\frac{1}{\kappa(2\kappa+\sigma^2)} - \frac{\exp(\kappa T)}{\kappa(\kappa+\sigma^2)} + \frac{\exp((2\kappa+\sigma^2)T)}{(2\kappa+\sigma^2)(\kappa+\sigma^2)}\right)\Bigg]^{-1/2} > 1. \qquad (5.6)
\end{aligned}$$

Remark: For either of these sufficient growth conditions, note that setting $a = 0$ results in the corresponding sufficient growth conditions for annuals, depending on if $r \neq \kappa$ (5.2) or if $r = \kappa$ (5.3).

5.3.2 A Few Graphs

Next, we draw some graphs of the left side of (5.5) and (5.6) to get an idea of how the different parameters affect how likely the sufficient growth condition is to be met. To aid us in the following discussion, we make the following definitions:

$$\begin{aligned} f_1(a,b,r,\kappa,\sigma,T) &= a^2 \cdot \exp(2(rT-\kappa(T-d_P))+\sigma^2 T) \\ &\quad + \frac{4ab\kappa}{2r+3\sigma^2}\left(\exp((2r+2\sigma^2)T)-\exp((r+(1/2)\sigma^2)T)\right) \\ &\quad + 2b^2\kappa^2\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right) \qquad (5.7) \\ F(a,b,r,\kappa,\sigma,T) &= \left(\exp(rT-\kappa(T-d_P))\left(a+\frac{b\kappa}{r-\kappa}\right)-\frac{b\kappa}{r-\kappa}\exp(rd_P)\right)^2 \cdot f_1^{-1/2} \end{aligned}$$

(5.8)

$$G(a,b,\kappa,\sigma,T) = ((a+b\kappa(T-d_P^*))\cdot\exp(\kappa d_P^*))^2 \cdot f_1(a,b,\kappa,\kappa,\sigma,T)^{-1/2}. \qquad (5.9)$$

Although not explicitly stated, we, of course, use d_P^* if $r=\kappa$ and d_P otherwise where appropriate. Thus, $F>1$ corresponds to (5.5) being satisfied and $G>1$ corresponds to (5.6) being satisfied; both F and G represent lower bounds on the median of $X_1\cdots X_n$.

Remark: If $r-(1/2)\sigma^2 \geq 0$, then we could instead define

$$\begin{aligned} f_2(a,b,r,\kappa,\sigma,T) &= a^2 \cdot \exp(2(rT-\kappa(T-d_P))+\sigma^2 T) \\ &\quad + \frac{2ab\kappa}{r+\sigma^2}\left(\exp((2r+\sigma^2)T)-\exp(rT)\right) \\ &\quad + 2b^2\kappa^2\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right) \qquad (5.10) \end{aligned}$$

and use this instead of f_1 in the definitions of F and G for a tighter bound. Since f_1 provides a universal bound, and, as we'll show in the next section, the only difference

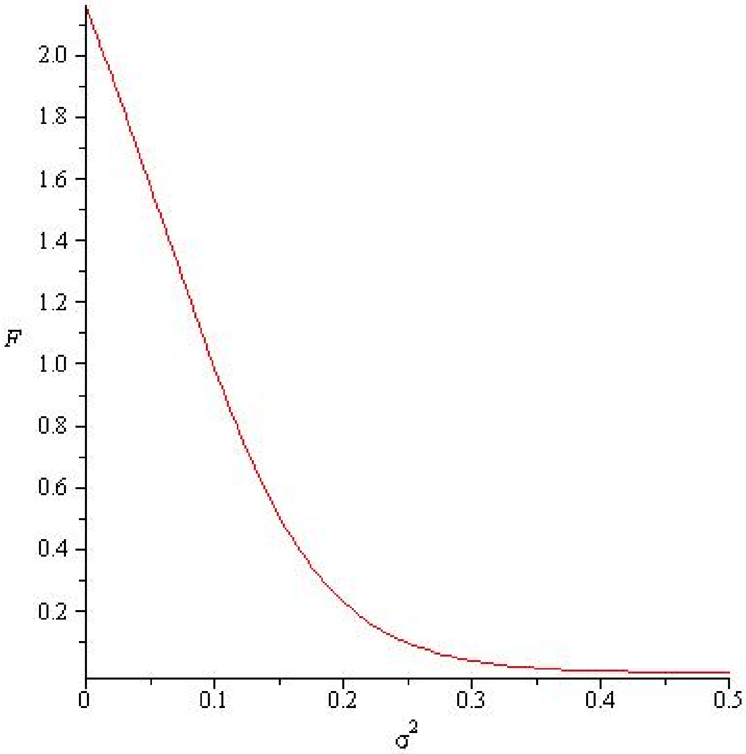

Figure 5.7: Comparing a median lower bound with volatility, σ^2

in long-term behavior between using f_1 and f_2 is when varying T, we will draw graphs using f_1 except when discussing T.

Let's begin by looking at F compared to σ^2. Figure 5.7 illustrates this, fixing $a = 0.6$, $b = 5$, $r = 0.03$, $\kappa = 0.1$, and $T = 20$. For Figure 5.7 and the other graphs in this section, we are most interested in where (5.5) is met; that is, any points on the curve where $F > 1$, since the true median is at least F. So, we note that, as σ^2 increases, F appears to decrease and approach 0; that is, the sufficient growth condition becomes much more unlikely to be met as the volatility increases. This makes sense biologically because, as previously discussed, increasing the volatility means making large swings in the environmental effects more common, both good and bad. Focusing on the bad swings, as those become larger and more common, the

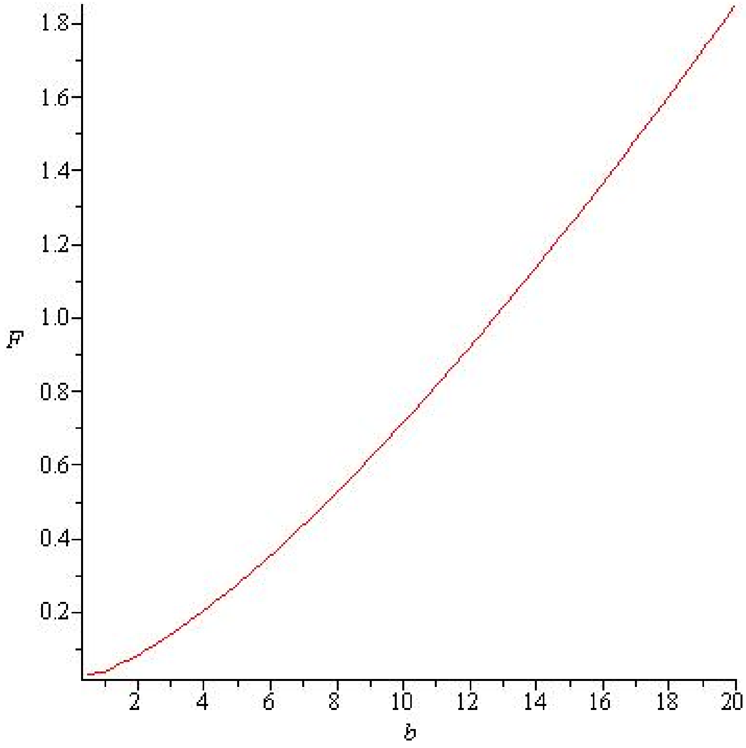

Figure 5.8: Comparing a median lower bound with reproductive utility, b

other (deterministic) parameters may not be enough to help the population overcome the detrimental effects of these swings, meaning that growth should become less likely over multiple seasons.

The asymptotic behavior of F with respect to σ (and the other parameters in this section) will be derived in the next section. Also, the graph of G with respect to σ^2 has exactly the same structure, and so we will omit it.

Next, we graph F compared to b. This is illustrated in Figure 5.8, fixing $a = 0.5$, $r = 0.05$, $\kappa = 0.1$, $T = 20$, and $\sigma^2 = 0.2$. This graph leads us to the fairly logical conclusion that increasing b leads to F increasing; in fact, F seems to become infinitely large as b does. Biologically, this says that, as the reproductive utility increases, the median (and hence the chances for long-term growth) should increase. This makes sense because, as b increases, reproduction begins sooner and goes for longer during the season (if season-long reproduction was not already occurring), which reduces the impact of bad environmental stretches. But, more importantly, any biomass invested in reproduction will then pay off more in the next season as b increases. Thus, a high b should result in a higher amount of biomass being invested into reproduction with a higher return for the following season.

The graph of G with respect to b has exactly the same structure, and so we will omit it.

Remark: Recall that, in this case, we assume that b is strictly larger than a, so we cannot consider what happens as b approaches 0 (the best we can do is what happens as b approaches a from above). This is why the graph drawn starts at $b = 0.5$.

Next, we graph F compared to r. Figure 5.9 illustrates this, fixing $a = 0.6$, $b = 10$, $\kappa = 0.05$, $T = 20$, and $\sigma^2 = 0.1$. From the graph, we observe that, as r becomes large, F appears to become infinitely large. This says that increasing the exponential growth rate of the plants is expected to increase the median. This certainly makes sense because, if the growth rate is increased, then the plants are not only better protected against bad swings in the environment, but they are also more likely to have large, persistent growth throughout the season. And, since increasing r also (usually) delays when reproduction begins, assuming T is fixed, the plants should have a lot more biomass able to invest in reproduction as well as plenty left over to carry over to the next season.

The next graph we consider compares F to κ. Figure 5.10 illustrates this, fixing $a = 0.6$, $b = 15$, $r = 0.05$, $T = 20$, and $\sigma^2 = 0.2$. Here, we notice that, as κ increases, the value of F initially increases, hits a peak, and then appears to decrease afterward to 0. Biologically, this says that we expect the chances for growth to initially increase as κ increases, and then begin to decline as κ increases further. This makes

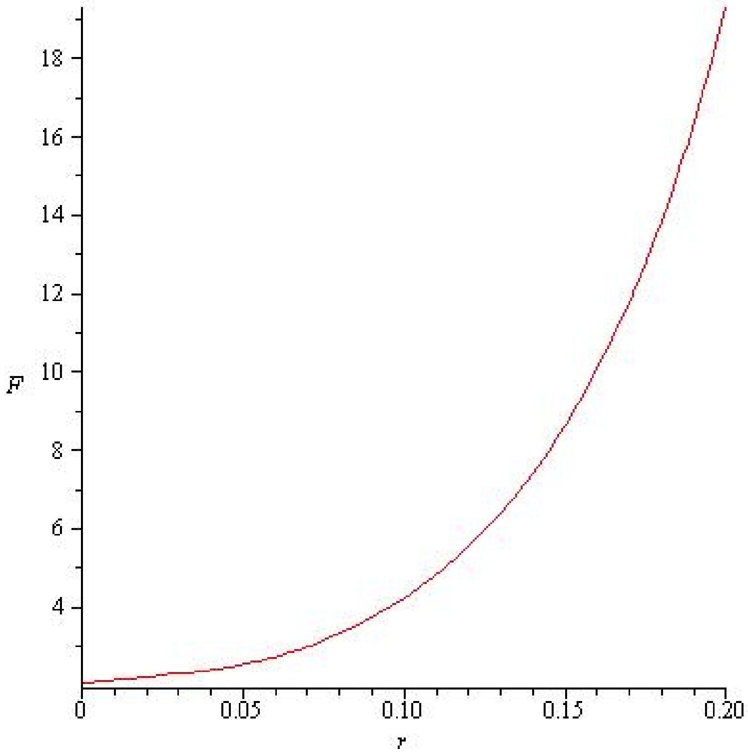

Figure 5.9: Comparing a median lower bound with growth rate, r

sense because, first off, a higher value of κ means more biomass can be devoted to reproduction at any given time, so increasing κ should result in a higher median since $b/a > 1$. But, as κ continues to increase, the plants begin “self-cannibalizing”, which means that any growth obtained from the plants’ intrinsic growth rate and what can be reasonably expected from the environment (plus more beyond that for very high values of κ) will be used for reproduction. This is expected to leave much less biomass for the plants to devote to reproduction or to stockpile to the next season since, in the next instant, there is expected to be less biomass than in the previous instant. Hence, for high values of κ, we expect that the median should decrease.

Next, we graph G compared to κ in Figure 5.11, fixing $a = 0.6$, $b = 1$, $T = 5$, and $\sigma^2 = 0.2$. Recall that, when considering G, $r = \kappa$, and so the behavior of G against

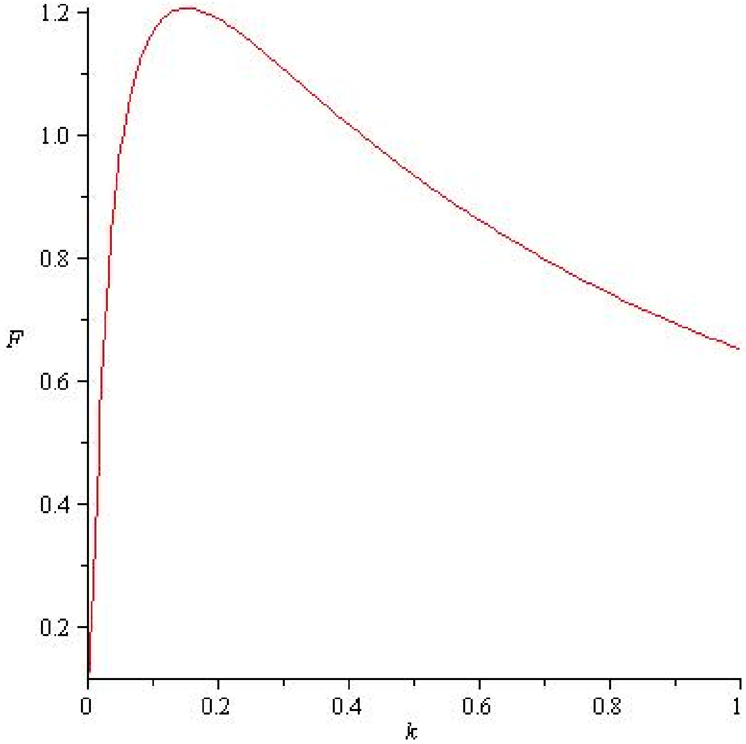

Figure 5.10: Comparing a median lower bound with maximum reproductive rate, κ

κ should be fundamentally different than what we observed with F since there is, by definition, no "self-cannibalization;" the only way the plant biomass can decay from instant to instant is due to the environment. Here, the long-term behavior of G is just like the long-term behavior of F with respect to r; that is, biologically, as κ increases, we expect the median to increase as well since, not only do we expect more biomass to be available for reproduction, but the plants are utilizing all biomass that grows intrinsically and nothing more. So, since the environmental effects have mean 0, the intrinsic growth rate is the main determining factor in whether we should expect growth or not.

Our final parameter to consider is T. As in the annuals case, there will be three possible behaviors of F as T becomes very large; however, here, we will use the tighter

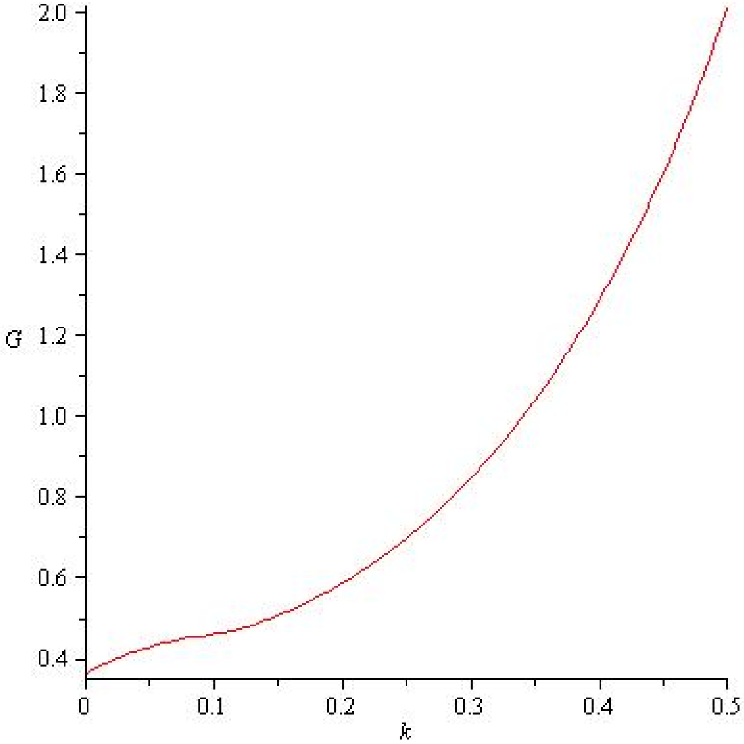

Figure 5.11: Comparing a median lower bound with maximum reproductive rate = growth rate, κ

bound of f_2 where appropriate (recall that, to use f_2, we require $r \geq (1/2)\sigma^2$) to illustrate this. For each of the graphs in Figure 5.12, we fix $a = 0.6$, $b = 10$, $\kappa = 0.05$, and $\sigma^2 = 0.2$; however, we fix $r = 0.03$ for the leftmost graph (we have to use f_1 for this graph), $r = 0.1$ for the middle graph, and $r = 0.12$ for the rightmost graph (we can use f_2 for these two). In the first scenario, we notice that, as T increases, F initially increases and then seems to decrease, eventually approaching 0. In the second scenario, F increases and eventually approaches a finite limit, but, in the third scenario, F appears to increase unboundedly. As the chosen parameter values suggest, determining which scenario occurs means comparing r and σ^2. Specifically, we have the following:

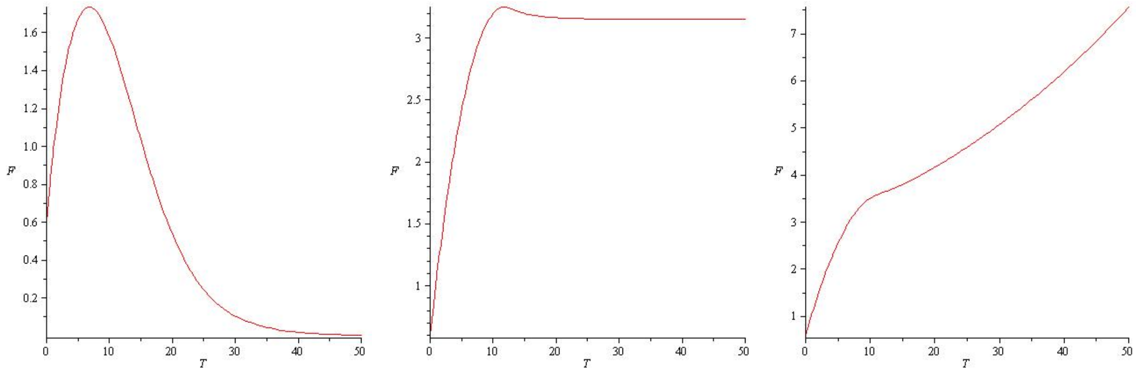

Figure 5.12: Comparing a median lower bound with season length, T ($r = 0.03$ for left graph, $r = 0.1$ for middle graph, $r = 0.12$ for right graph)

- If $r < (1/2)\sigma^2$, the first scenario occurs.
- If $r = (1/2)\sigma^2$, the second scenario occurs.
- If $r > (1/2)\sigma^2$, the third scenario occurs.

This is exactly the same result that we obtained in the annuals case. However, it is worth noting that, if one uses f_1 universally, then the above result changes to how r compares to σ^2.

The biological explanation for why this occurs is exactly the same as for annuals, and so we refer the reader to Section 5.2.2 for this explanation. Also, the long-term behavior of G with respect to T is the same as for F, and so we will omit its graphs.

Analyzing what happens to the graphs with respect to a will actually help us answer the second question at the beginning of Chapter 5; hence, we will save this for Section 5.4.

Remark: It is important to note that, depending on the other parameter values, it is possible for the graphs of F and/or G against σ^2, κ, and/or T (when $r < (1/2)\sigma^2$) to never exceed 1. In these cases, the sufficient growth condition tells us nothing mathematically useful about the actual median.

5.3.3 Analytic Properties of Sufficient Growth Condition

We now mathematically prove some of the properties of the sufficient growth condition (5.5) or (5.6) that were discussed in the previous section. However, because the computations are very similar to those done in Case 2, and the expressions are much longer and messier here, most of the proofs will be sketches.

In all of these discussions, we consider the lower bounds on the median of $X_1 \cdots X_n$ that we derived in Section 5.3.1; namely,

$$F(a,b,r,\kappa,\sigma,T) = \left(\exp(rT-\kappa(T-d_P))\left(a+\frac{b\kappa}{r-\kappa}\right)-\frac{b\kappa}{r-\kappa}\exp(rd_P)\right)^2 \cdot f_1^{-1/2}$$

$$G(a,b,\kappa,\sigma,T) = ((a+b\kappa(T-d_P^*))\cdot\exp(\kappa d_P^*))^2\cdot f_1(a,b,\kappa,\kappa,\sigma,T)^{-1/2}.$$

The first property we will prove is that, as the volatility, σ, becomes large, then the lower bound on the median will approach 0. To do this, in both the expressions for F and G, we want to compute

$$\lim_{\sigma\to\infty} f_1(a,b,r,\kappa,\sigma,T)$$

since this is the only piece of both F and G that is dependent on σ. Now, since

$$\begin{aligned} f_1(a,b,r,\kappa,\sigma,T) = {} & a^2\cdot\exp(2(rT-\kappa(T-d_P))+\sigma^2T) \\ & + \frac{4ab\kappa}{2r+3\sigma^2}\left(\exp((2r+2\sigma^2)T)-\exp((r+(1/2)\sigma^2)T)\right) \\ & + 2b^2\kappa^2\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right), \end{aligned}$$

then it is clear that $\lim_{\sigma\to\infty} f_1 = \infty$ since, as σ becomes very large, each term of f_1 will either go to 0 or be dominated by the exponential term that is a factor of it (ex. $\frac{1}{(2r+\sigma^2)(r+\sigma^2)}\exp((2r+\sigma^2)T)$ is dominated by $\exp(\sigma^2T)$ for large σ). This implies that

f_1 becomes infinitely large, which then implies that F and G go to 0, and in fact should do so exponentially since both are proportional to $f_1^{-1/2}$.

Remark 1: It is worth noting that, although f_1 has a finite limit as σ approaches 0, the limit is not correct, as it is not equal to the value that would actually be achieved if there was no variance (see Section 3.3). This is due to the estimates used from Yor. Also, this argument does not change if

$$\begin{aligned} f_2(a,b,r,\kappa,\sigma,T) &= a^2 \cdot \exp(2(rT-\kappa(T-d_P))+\sigma^2 T) \\ &+ \frac{2ab\kappa}{r+\sigma^2}\left(\exp((2r+\sigma^2)T)-\exp(rT)\right) \\ &+ 2b^2\kappa^2\left(\frac{1}{r(2r+\sigma^2)}-\frac{\exp(rT)}{r(r+\sigma^2)}+\frac{\exp((2r+\sigma^2)T)}{(2r+\sigma^2)(r+\sigma^2)}\right) \end{aligned}$$

is used when appropriate ($r \geq (1/2)\sigma^2$).

Remark 2: Since we've shown that a *lower bound* on the median approaches 0, it is certainly worth noting that the true median may not follow suit. Biologically, it certainly makes sense that this would happen, but, mathematically, all we can say is that, since this lower bound goes to 0, for large values of σ, this does not necessarily tell us anything useful about the actual median.

Next, we will show that, as the utility factor, b, becomes large, then the lower bound on the median will do the same. Recalling that $\lim_{b\to\infty} d_P = d_A$ and $\lim_{b\to\infty} d_P^* = d_A^*$, we then see that the exponential functions present in F and G will all be bounded as b becomes very large since d_A and d_A^* are finite by definition. Because of this, we only need to consider that the dominant term in f_1 (or f_2) is of the form b^2, and the dominant term for the first part of each of F and G is also of the form b^2. Since the b^2 term in the first part of F is

$$b^2\left(\frac{\kappa}{r-\kappa}\right)^2\left(\exp(rT-\kappa(T-d_P)-\exp(rd_P))\right)^2 \geq 0,$$

then it follows that $\lim_{b\to\infty} F = \infty$. Likewise, since the b^2 term in the first part of G is

$$b^2(\kappa(T - d_P^*))^2 \cdot \exp(2\kappa d_P^*) \geq 0,$$

then it follows that $\lim_{b\to\infty} G = \infty$. From this, we observe that both F and G should increase linearly to infinity. More importantly, as b increases, the median must also increase to infinity since F and G represent lower bounds on the median. Because of this, for any choice of the other parameter values, then there must exist some value of b (say, b^*) that ensures that the median is at least 1 (ensuring at least a 50% chance for growth) for any $b > b^*$.

Remark: It is again worth noting that, if one were to observe F and G as b approaches a, the expected limit would not be attained (by Lemma 3.4, no reproduction would be taking place, so all but the first term in f_1 or f_2 should drop out, but this clearly doesn't happen); this is again due to the estimates used from Yor.

Next, we will show that, as the intrinsic growth rate, r, becomes very large, then the lower bound on the median will do the same. Using the expressions above, and noting that $r = \kappa$ when using G, we first note that

$$\lim_{r\to\infty} T - \frac{1}{r-\kappa} \ln\left(\frac{br}{a(r-\kappa) + b\kappa}\right) = \lim_{\kappa\to\infty} T - \frac{b-a}{b\kappa} = T.$$

This says that, as r becomes very large, virtually no time during the season is spent reproducing. With this in mind, we notice that, as r becomes very large, the dominant terms in the first parts of F and G will be of the form $\exp(2rT)$, and the dominant terms in f_1 (or f_2) will also be of the form $\exp(2rT)$. Hence, F and G increase exponentially as r (κ when considering G) becomes large, and $\lim_{r\to\infty} F = \lim_{\kappa\to\infty} G = \infty$. Thus, just like for b, for any choice of the other parameter values, there must exist some value of r, say, r^* (κ when considering G) that ensures the median is at least 1 for any $r > r^*$.

The next parameter we will consider is the maximum reproductive rate, κ. We want to show that, if $r \neq \kappa$, then, as κ becomes very large, the lower bound on the median will approach 0 (the case where $r = \kappa$ is addressed above). So, we first note that

$$\lim_{\kappa \to \infty} T - \frac{1}{r-\kappa} \ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right) = T.$$

Thus, for sufficiently large κ, virtually no time is spent reproducing during the season. In fact, this says that $\lim_{\kappa \to \infty} \kappa(T - d_P)$ is an indeterminate form, and so we turn to l'Hospital's Rule to evaluate it:

$$\begin{aligned}
\lim_{\kappa \to \infty} \kappa(T - d_P) &= \lim_{\kappa \to \infty} \frac{\frac{1}{r-\kappa} \ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right)}{(1/\kappa)} \\
&= \lim_{\kappa \to \infty} -\frac{\kappa^2}{(r-\kappa)^2} \ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right) + \frac{\kappa^2(b-a)}{(r-\kappa)(a(r-\kappa)+b\kappa)} \\
&= \infty
\end{aligned}$$

since the second term goes to -1 and the first term goes to infinity (the natural log quantity goes to negative infinity). This says that any quantity of the form $\exp(-\kappa(T - d_P))$ goes to 0 as κ approaches infinity. Thus, the first part of F goes to 0 and does so exponentially (like $\exp(-2\kappa(T - d_P))$), while f_1 (and f_2) goes to infinity like κ^2, meaning, indeed, $\lim_{\kappa \to \infty} F = 0$, and this is approached exponentially. Of course, we have to keep in mind that, by definition, $\kappa < 1 + r$, so κ can never get infinitely large according to the model; however, this does give us an idea of what could happen if we continue to increase κ, since, in this case, we don't get anything necessarily useful about the actual median.

Remark: It is also worth noting that

$$\lim_{\kappa \to 0^+} F = a \cdot \exp(rT - (1/2)\sigma^2),$$

which, unlike the previous cases, *is* the limit we would expect, since this is the median from Case 1, where no reproduction takes place. This can be easily verified by direct substitution and noting that

$$\lim_{\kappa \to 0^+} T - \frac{1}{r-\kappa} \ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right) = T - \frac{1}{r}\ln\left(\frac{b}{a}\right).$$

Also, in the case where $r = \kappa$, by using l'Hospital's Rule and that $\lim_{\kappa \to 0^+} T - \frac{b-a}{b\kappa} = -\infty$, and hence $\lim_{\kappa \to 0^+} d_P^* = 0$, it can be shown that

$$\lim_{\kappa \to 0^+} G = a \cdot \exp(-(1/2)\sigma^2).$$

This, again, is the limit we would expect to occur.

The final parameter we will consider is the season length, T. We want to show that, depending on the relationship between r and σ^2, we can end up with three different limits for F and G. For the following discussion, since there is a difference in behavior depending on whether f_1 or f_2 is used, we use f_2 where it can be used (whenever $r \geq (1/2)\sigma^2$) since it makes F or G a tighter lower bound than f_1.

Clearly, as T becomes very large, so will $T - \frac{1}{r-\kappa}\ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right)$ and $T - \frac{b-a}{b\kappa}$, so we can assume that d_P and d_P^* are each nonzero. Hence, $T - d_P$ is not dependent on T and has a fixed, positive value for large T (see Remark 2 after Theorem 3.5). So, let $\delta > 0$ be given. We first want to check that, when $r = (1/2)\sigma^2 + \delta$, both F and G (use $\kappa = (1/2)\sigma^2 + \delta$) becomes infinitely large as T becomes infinitely large.

So, we plug in $r = (1/2)\sigma^2 + \delta$ into f_2 and note that, as T becomes very large, the dominant term of f_2 is of the form $\exp((2\sigma^2 + 2\delta)T)$, and hence $f_2^{1/2}$ contributes a dominant term of the form $\exp((\sigma^2 + \delta^2)T)$. Observing that the first parts of F and G have dominant term of the form $\exp((\sigma^2 + 2\delta)T)$ for this choice of r, we have that, again,

$$\lim_{T \to \infty} F = \lim_{T \to \infty} G = \infty.$$

So, as long as $r > (1/2)\sigma^2$, then we see that both F and G will increase exponentially as T becomes very large. Hence, there must exist a value of T, say, T^*, such that, whenever $T > T^*$, the median must be greater than 1.

Remark: Should $r > \sigma^2$, a similar argument can be used to show that, under f_1, both F and G will increase exponentially to infinity as T increases to infinity.

On the other hand, if we plug in $r = (1/2)\sigma^2 - \delta$ into f_1 (f_2 cannot be used here) and assume that $0 < \delta < (1/2)\sigma^2$ (this is so $r > 0$), then we see that, as T becomes very large, the dominant term of $f_1^{1/2}$ is of the form $\exp((3/2)\sigma^2 - \delta)T)$. We also observe that the first parts of both F and G have dominant term of the form $\exp((\sigma^2 - 2\delta)T)$. Thus,

$$\lim_{T \to \infty} F = \lim_{T \to \infty} G = 0$$

whenever $r < (1/2)\sigma^2$, and both will, in fact, decrease exponentially to this limit. Unfortunately, as was the case with σ^2 and κ, this does not allow us to say anything definitive about the actual median here.

Finally, if we plug in $r = (1/2)\sigma^2$, using the above work, it is clear that the dominant term of $f_2^{1/2}$ will be of the form $\exp(\sigma^2 T)$ and the dominant term in the first parts of F and G will be of the form $\exp(\sigma^2 T)$ as well. Hence, in this case, both F and G approach finite values as T approaches infinity.

5.4 Annuals vs. Perennials

We now attempt to answer the second question posed at the beginning of this chapter; namely, "Under what condition(s) are annuals favored over perennials (or vice versa)?" To do this, we use the lower bounds on the median of $X_1 \cdots X_n$, F (5.8) and G (5.9) found earlier and draw contour plots of them, taking a, the average survivorship of adult perennials from one season to the next, as the independent variable. We want to see what happens as we increase each of the other parameters while fixing the others; specifically, is F (or G) higher when $a = 0$ (annuals) or when $a > 0$ (perennials)? Or, put another way, do annuals or perennials appear to have a higher chance of long-term growth?

Of course, since these are estimates, these will not say for absolute certainty which of the two are better, but they will give us some indication as to the effects of the different parameters on whether annuals or perennials should be more likely to persist over the long run.

For each of these discussions, we will draw only the graphs of F, since experimentation on Maple showed that the graphs of G all result in the same overall conclusions as the corresponding graphs of F. Likewise, we will only be using f_1 (5.7) here since experimentation showed that using f_2 (5.10) where appropriate did not provide any different overall conclusions than f_1. Recall that, if one sets $a = 0$ in F or G, then we end up with the corresponding lower bound on the median of $X_1 \cdots X_n$ in the annuals case, which is not only exactly what we'd expect, but is imperative to this analysis. In order to obtain a direct comparison between annuals and perennials when reproduction takes place, we take $b > 1$ for all of these graphs since, by definition, $0 \leq a \leq 1$, and we want $b/a > 1$ to ensure that the perennials will reproduce.

The first parameter we consider is the environmental volatility, σ. Figure 5.13

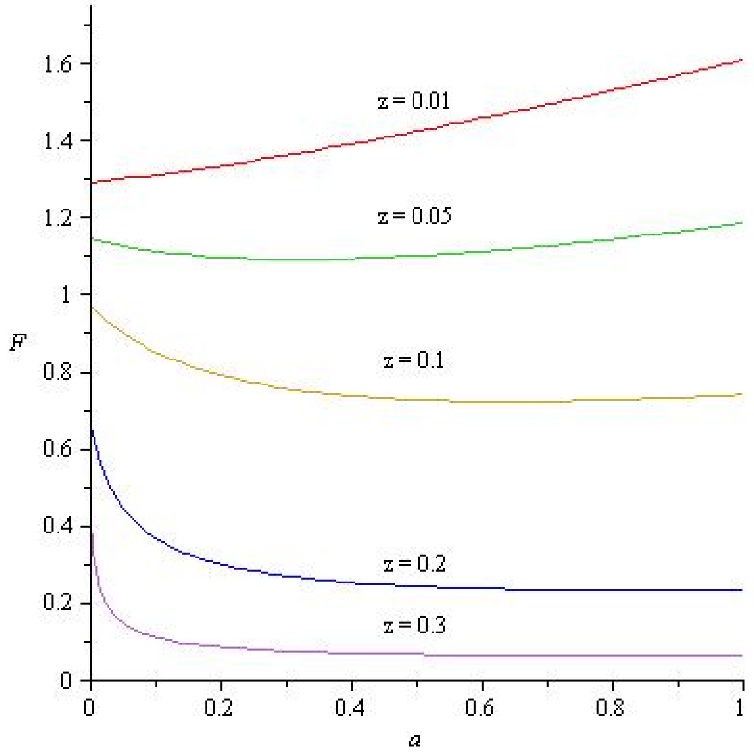

Figure 5.13: Annuals vs. Perennials with respect to volatility, σ^2

shows a contour plot, graphing F compared with a for different chosen values of σ^2 while fixing $b = 3$, $r = 0.03$, $\kappa = 0.05$, and $T = 15$. For this graph only, we set $z = \sigma^2$ for ease in labeling the contours. Looking at the graph, we first notice that, as σ increases, the estimated median decreases, regardless of the value of a, as we would anticipate from Figure 5.7. More importantly, however, we notice that, for sufficiently high values of σ, annuals appear to be favored (the contours have their peak at $a = 0$), while, for sufficiently low values of σ, perennials appear to be favored (the value of F is higher for all values of $a > 0$ than at $a = 0$). In-between these values of σ, however, it is possible for perennials to be favored, depending on the value of a (annuals appear to be favored when a is low, but perennials appear to be favored when a is high). This makes biological sense since, although large swings in the environment can help or hurt both perennials and annuals, they make their reproductive decisions independent of the environment. In fact, it is worth noting that, if all parameters except a, b are fixed,

$$\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right) > \frac{1}{r-\kappa}\ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right).$$

This is clearly true if $r > \kappa$ since, in that case, we'd have

$$\frac{br}{a(r-\kappa)+b\kappa} < \frac{r}{\kappa}.$$

If $r < \kappa$, then this inequality flips, but, since $1/(r-\kappa)$ is negative in this case, then the claim still holds. Hence, we have that $d_A \leq d_P$ when all except a, b are fixed. So, for any choice of a, b, perennials will wait longer during the season to begin reproduction than annuals will, or will begin reproduction at the same time. This makes sense biologically because perennials are able to carry over some of their adult biomass into the next season. But, with a high volatility, devastating swings in the environment become more common, which are more likely to happen to perennials if they wait longer to begin reproduction. Thus, annuals should be more likely to have long-term growth in highly volatile environments than perennials, all other parameters being equal.

It can also clearly be seen that

$$\frac{b-a}{b\kappa} < \frac{1}{\kappa}$$

for any fixed choice of κ, and hence, if κ, T are fixed, it follows that $d_A^* \leq d_P^*$. Hence, for any choice of a or b, annuals begin reproducing when, or before, perennials do when $r = \kappa$ as well.

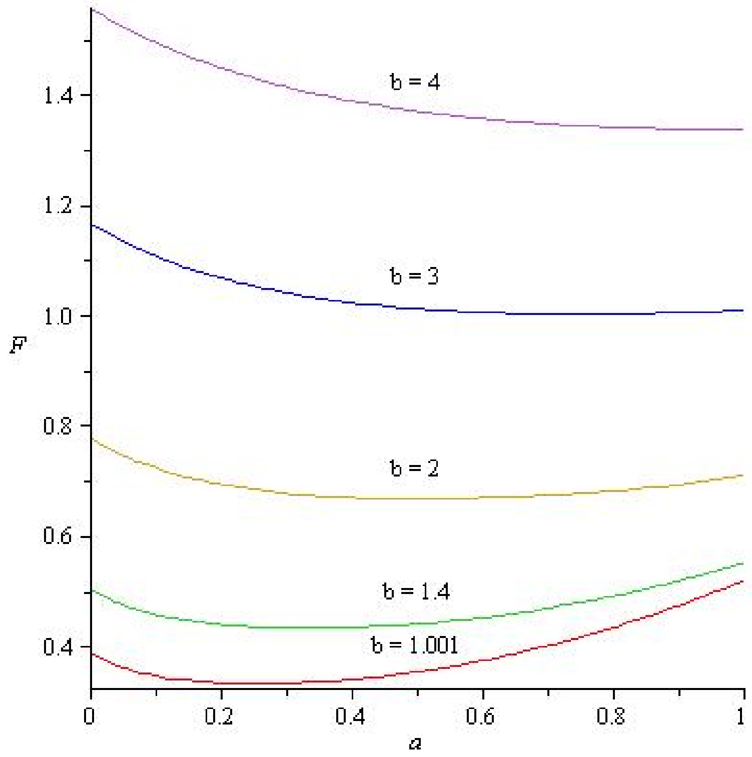

Figure 5.14: Annuals vs. Perennials with respect to b

The next parameter we consider is the reproductive utility, b. Figure 5.14 shows a contour plot of F compared with a, fixing $r = 0.05$, $\kappa = 0.1$, $\sigma^2 = 0.1$, and $T = 10$. From this graph, we notice that, regardless of the value of a, higher values of b lead to an increase of F, as we would anticipate from Figure 5.8. More importantly, sufficiently high values of b appear to favor annuals, and sufficiently low values of b appear to favor perennials; however, this also depends on a since, if a is sufficiently small, then annuals appear to still be favored. Biologically, this makes sense considering how much more important the utility of seeds is to annuals since the only way that they can bring biomass into the next season is to reproduce; this is further evidenced by the fact that their reproductive strategy has no dependence on b. Also, since, assuming r, T, and κ are fixed, perennials will either begin to reproduce at the same

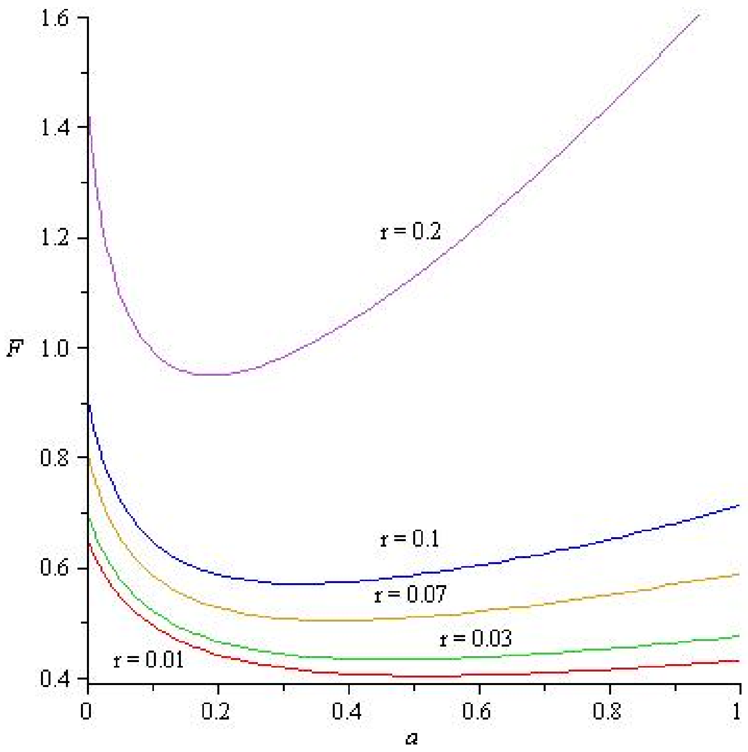

Figure 5.15: Annuals vs. Perennials with respect to growth rate, r

time as annuals or wait longer before beginning to reproduce (we also observed in Section 3.4 that, as b increases, so does d_P). So, a very high utility factor is something that annuals may be able to take advantage of a lot sooner, and, presumably, with more available biomass than the perennials will since perennials play against the risky environment longer with hence a greater chance of smaller gains, or even losses. So, if the adult season-to-season survivorship is too low, it is reasonable to assume that perennials may not have as much long-term yield as annuals would.

The next parameter we consider is the growth rate, r. The contour plot of F compared with a is drawn in Figure 5.15, fixing $\kappa = 0.05$, $b = 3$, $\sigma^2 = 0.2$, and $T = 10$. From this graph, we observe that, regardless of the value of a, increasing r generally results in an increase of F, as we would anticipate from Figure 5.9. More importantly, it appears that sufficiently high values of r favor perennials (assuming a sufficiently high a as well), and sufficiently low values of r appear to favor annuals. Biologically, this makes sense because an increased intrinsic growth rate will help soften the effects of bad environmental swings as well as enhance good ones. Since perennials can save some of their adult biomass for the following season, but annuals cannot, increasing r should give the perennials a good "head start" the following season since it would be expected they would carry over a large quantity of adult biomass. The observation that a sufficiently low a seems to favor annuals comes from the fact that, fixing all parameters except r,

$$\frac{1}{r-\kappa}\ln\left(\frac{br}{a(r-\kappa)+b\kappa}\right)=\frac{1}{r-\kappa}\ln\left(\frac{r}{(a/b)(r-\kappa)+\kappa}\right)<\frac{1}{r-\kappa}\ln\left(\frac{r}{\kappa}\right).$$

Thus, $d_A \leq d_P$ here; it is also easy to check that $d_A^* \leq d_P^*$, taking $r = \kappa$. So, for a sufficiently low value of a, the perennials will most likely wait longer to reproduce than annuals, especially if r is high (see Section 3.4); this again allows for a higher risk of potentially catastrophic environmental swings which can wipe out any gains from the high growth rate. With a low a, it is possible that not a lot of reproduction will occur, and very little adult biomass will carry over to the following season, thus appearing to favor annuals.

Next, we consider the maximum reproductive rate, κ. Fixing $r = 0.04$, $b = 5$, $\sigma^2 = 0.15$, and $T = 20$, we sketch the contour plot comparing F with a in Figure 5.16. From this graph, we observe that the value of F with regards to κ takes on strange behavior, depending on the value of a. Since initially increasing κ generally increases F (there is a slight anomaly on this graph for high values of a and low values of κ where this doesn't occur, but this does not happen in general), but then decreases it due to the "self-cannibalization" effect, we see these contours colliding. Looking at

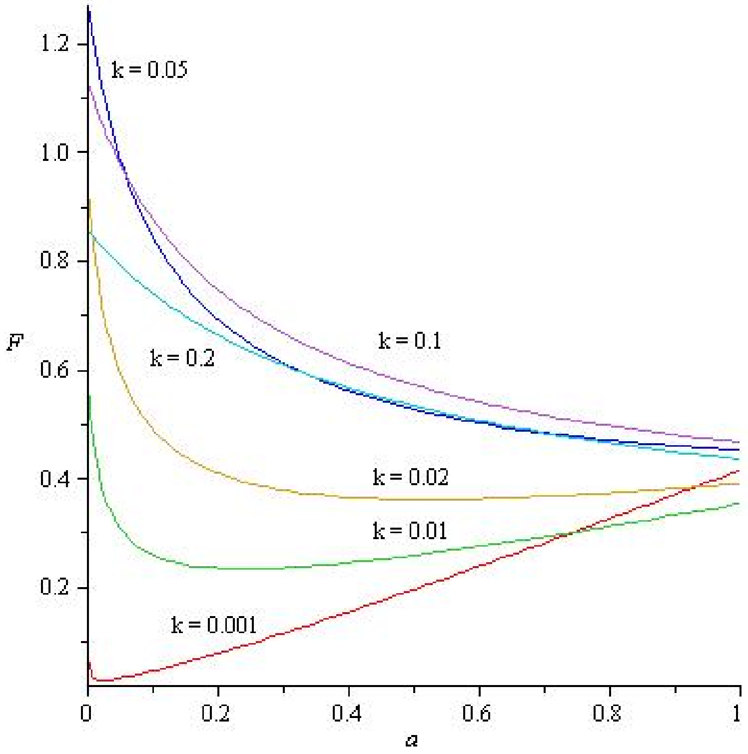

Figure 5.16: Annuals vs. Perennials with respect to maximum reproductive rate, κ

the contours, though, it appears that sufficiently high values of κ favor annuals, and sufficiently low values of κ appear to favor perennials, pending a is also sufficiently high.

This, again, makes sense biologically considering that annuals have to reproduce, and perennials don't. If the plants aren't allowed to devote a lot of their biomass to reproduction at any given instant, this is expected to put annuals at a disadvantage since perennials can carry over adult biomass into the next season. Since this is the main advantage of perennials, though, it also makes sense that having a be too low would make this advantage almost nothing, giving the advantage back to annuals since, all parameters except κ fixed, perennials begin reproduction when, or after, annuals (same argument as for r). On the other hand, allowing the plants to devote

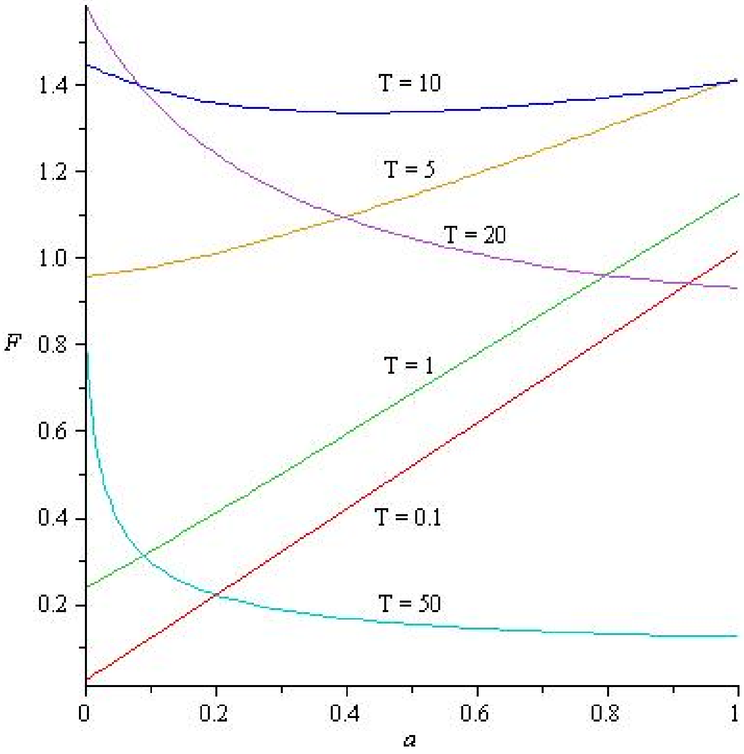

Figure 5.17: Annuals vs. Perennials with respect to season length, T

large quantities of biomass to reproduction should favor annuals since they begin reproduction when, or before, perennials do, so it is expected that they should get more biomass into the following season and, with a good utility rate, should experience more growth than the perennials.

Finally, we consider the season length, T. Although, as proven previously, there are three possible cases for how F changes with respect to increasing T, experimentation on Maple showed that, regardless of which case prevails, the overall effect of T on whether annuals or perennials seem to be favored is the same. Hence, we will only draw the graph for one case here.

So, fixing $r = 0.03$, $\kappa = 0.05$, $b = 5$, and $\sigma^2 = 0.1$, we sketch a contour plot comparing F with a in Figure 5.17. Looking at this graph, it seems that sufficiently low values of T favor perennials, and sufficiently high values of T favor annuals. There are also some values of T in-between these which appear to favor perennials, pending a is sufficiently high. Low values of T favoring perennials certainly makes biological sense because, if the season is very short, the annuals won't have much time to devote biomass to reproduction, whereas the perennials won't need to since they can carry over some of their adult biomass into the next season. High values of T favoring annuals also makes biological sense because, with a long season, a growing period is expected to occur at the beginning of the season. But, since perennials begin reproduction after, or at the same time as, annuals (fixing all other parameters except T), a longer season also means more risk. So, for example, a high enough volatility could mean large losses for the perennials since they could have a higher risk for large losses, and hence perennials may not have as much to devote to reproduction and not enough adult biomass to carry over to make up the difference.

So, in summary, via this analysis, annuals are expected to be favored over perennials (that is, annuals are expected to be more likely to experience long-term growth than perennials) if one or more of the following conditions hold:

- The environmental volatility is sufficiently high.
- The utility factor of seeds is sufficiently high.
- The intrinsic growth rate is sufficiently small.
- The maximum proportion to be devoted to reproduction at any instant is sufficiently high.
- The season is sufficiently long.
- The season-to-season survivorship of adult perennials is sufficiently low, pending one or more of the previous conditions are met.

Chapter 6

Some MATLAB Results

In this chapter, we present some simulation work, done on MATLAB. The first set of simulations are meant to numerically verify, given some parameter values, that the optimal strategies found in Chapter 4 are indeed optimal in terms of expected value for (2.2 - 2.4). We'll compare the strategies from Chapter 4 with a handful of other strategies. Because these are numerical simulations of stochastic processes, however, variation will be involved as well; hence, we also list the standard deviation of the results for each set of trials to get an idea of the overall spread of the results for each strategy.

The second set of simulations assumes, instead of exponential growth, that logistic growth occurs. That is, assuming $r > 0$ is the logistic growth rate and $K > 0$ is the carrying capacity of the population, the biomass is subject to the SDE

$$dW_t = rW_t\left(1 - \frac{W_t}{K}\right)dt - \gamma(t)W_t dt + \sigma W_t dB_t. \tag{6.1}$$

For these simulations, we attempt to get an idea of what choice for $\gamma(t)$ might be optimal, and see how the choice depends on K.

Finally, we run these simulations, assuming optimal choices for $\gamma(t)$ (in the logistic case, we will make estimates based on the prior simulation results), over 100 seasons to see how the multiseason analysis performed in Chapter 5 compares with the numerical results. We'll then repeat the work with logistic growth to see the differences, especially when changing K.

For all of these simulations, the basic underlying concept is numerically approximating a solution to an SDE. To do so, we use Milstein's approximation method (see, for example, [12]; this is also briefly discussed in Appendix A), which, theoretically, is the stochastic equivalent of the deterministic Euler's method, as both have strong convergence of order 1. What the programs, detailed in Appendix A for the interested reader, will do is create an approximation of a sample path of the solution to the SDE (recall that a solution to an SDE is a random variable). Since T will always be between 10 and 30 for these simulations, we'll take a step size of $T/1000$ so that we get a fairly decent approximation to a sample path.

Naturally, we want to know how many sample paths we'll need to generate in order to be fairly confident in our results. To do this, we'll first define a successful run to be a run (single or multiseason) such that at least W_0 biomass will be present at the beginning of the next season. To have 95% confidence in measuring the probability of success with at most 5% error, note that, if

$$\begin{aligned} n &= \text{number of runs} \\ p &= \text{true probability of success} \\ \hat{p} &= \text{observed proportion of successes} \\ S_n &= \text{observed number of successes,} \end{aligned}$$

then we need, assuming n is sufficiently large so the Central Limit Theorem applies,

$$P\left(-1.96 < \frac{S_n - np}{\sqrt{np(1-p)}} < 1.96\right) \approx 0.95$$
$$P\left(-1.96\left(\sqrt{\frac{p(1-p)}{n}}\right) < \hat{p} - p < 1.96\left(\sqrt{\frac{p(1-p)}{n}}\right)\right) \approx 0.95.$$

The 1.96 bounds in the probablity come from a normal distribution table (see, for example, [13, p. 656]). However, since $0 \leq p(1-p) \leq 0.25$, then we want:

$$P\left(-0.98\frac{1}{\sqrt{n}} < \hat{p} - p < 0.98\frac{1}{\sqrt{n}}\right) \approx 0.95.$$

Setting $0.98/\sqrt{n} \leq 0.05$ for the 5% error, then note that we need $n \geq 368.64$ in order to have this level of accuracy for measuring the success probability. For simplicity, however, we will set $n = 1,000$ for all of the simulations to follow (this actually results in about 3.1% error).

We begin with some single-season simulations to verify that the optimal strategies we found in Chapter 4 are indeed optimal. So, first, we take $r = 0.03$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.1$, $a = 0.8$, $b = 2$, and $W_0 = 1000$ (in fact, we'll take $W_0 = 1000$ in all of the following simulations). This results in the optimal strategy $\gamma^*(t) = \kappa\bar{H}(t - d_P)$, where $d_P \approx 7.493$ here. So, indeed, the simulations in Table 6.1 confirm that $\gamma^*(t) = \kappa\bar{H}(t - d_P)$ should be an optimal control in terms of average (i.e., expected) value. However, note that the corresponding standard deviation is quite high in comparison to some of the other strategies.

Although only one set of simulations is given in Table 6.1 and those to follow, extra sets of simulations were done to confirm accuracy of the reported results. In fact, when doing these extra sets of simulations, there were occasions where the average value for $\gamma(t) = \kappa\bar{H}(t - 6)$ exceeded that of $\gamma^*(t)$. This is due to the natural

Gamma	**Avg. Value**	**Std. Dev.**
0	1407.2	953.5
$\kappa \bar{H}(6-t)$	1767.2	707.5
$\kappa \bar{H}(d_P-t)$	1875.3	698.6
$\kappa \bar{H}(13-t)$	2132.7	756.9
κ from 4 to 11	1984.8	943.9
0 from d_P to 18	2050.5	839.9
κ	2346.0	825.8
$\kappa \bar{H}(t-6)$	2491.0	1283.6
$\kappa \bar{H}(t-15)$	2234.5	1675.1
$\kappa \bar{H}(t-d_P)$	2539.5	1380.4

Table 6.1: Exponential growth for perennials without season-long reproduction

variability in the sample mean, the fact that 6 is pretty close to d_P in this case, and the fact that the standard deviation for the values corresponding to $\gamma^*(t)$ is quite large compared to the average value. This does not disprove that $\gamma^*(t)$ is an optimal control since we have the analytic work to back it up (Theorem 4.6 in Section 4.2), but it does indicate a potential pitfall of relying solely on simulations to determine an optimal control.

Experiments with smaller step sizes (1,000 steps vs. 10,000 steps) and more trials (1,000 vs. 2,000 vs. 10,000) did not change the overall observations above. Interestingly, even with more trials, the standard deviations did not vary too much from what they were with 1,000 trials; some simulations actually resulted in a slight increase in the standard deviation! This is most likely due to the natural variation present in Geometric Brownian Motion (see Section 5.1, for example), and/or it may be due to our choice of using the probability of success and not a measure based on the mean to determine the number of trials we should take.

These were observed with every simulation to follow as well, and so we will omit discussion of this from here on out. However, it is something the reader should keep in mind if he/she wishes to replicate these findings.

Gamma	**Avg. Value**	**Std. Dev.**
0	1449.1	1019.8
$\kappa\bar{H}(1-t)$	1219.5	591.7
$\kappa\bar{H}(6-t)$	1651.9	528.2
$\kappa\bar{H}(10-t)$	1857.9	587.5
κ from 2 to 9	1725.3	618.9
0 from 5 to 9	1811.4	590.5
$\kappa\bar{H}(t-2)$	1973.2	721.8
$\kappa\bar{H}(t-6)$	1826.1	892.6
$\kappa\bar{H}(t-10)$	1392.8	720.5
κ	1975.1	625.8

Table 6.2: Exponential growth for perennials with season-long reproduction

Gamma	**Avg. Value**	**Std. Dev.**
$\kappa\bar{H}(5-t)$	1425.6	266.8
$\kappa\bar{H}(d_A-t)$	2116.3	483.2
$\kappa\bar{H}(12-t)$	2253.8	568.5
κ from 5 to 15	2729.0	1204.0
0 from d_A to 18	2267.2	564.2
κ	2356.4	699.3
$\kappa\bar{H}(t-5)$	3055.8	1371.5
$\kappa\bar{H}(t-12)$	3262.1	1985.4
$\kappa\bar{H}(t-d_A)$	3405.8	1958.9

Table 6.3: Exponential growth for annuals with $r \neq \kappa$

Next, we take all of the same parameter values as in the previous simulation, but we'll make $T = 12$ so that $d_P = 0$ here, meaning $\gamma^*(t) = \kappa$ is the optimal strategy. We'll also have to look at slightly different choices for $\gamma(t)$ thanks to the changed value of T. Indeed, from Table 6.2, it appears that $\gamma^*(t) = \kappa$ is an optimal control.

Next, we consider an annual population ($a = 0$), taking $r = 0.05$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.2$, and $b = 2$. This results in the optimal strategy $\gamma^*(t) = \kappa\bar{H}(t-d_A)$, where $d_A \approx 10.758$ here. Again, Table 6.3 indicates $\gamma^*(t) = \kappa\bar{H}(t-d_A)$ does appear to be an optimal control. Note that we did not look at the strategy $\gamma(t) = 0$ here because, since this is the annuals case, if no reproduction occurs, obviously, there

Gamma	**Avg. Value**	**Std. Dev.**
$\kappa\bar{H}(5-t)$	1010.8	199.9
$\kappa\bar{H}(d_A^*-t)$	2028.2	568.4
$\kappa\bar{H}(12-t)$	2411.0	741.6
κ from 5 to 15	3271.4	1530.3
0 from d_A^* to 18	2929.7	1029.4
κ	4012.1	1596.4
$\kappa\bar{H}(t-5)$	4957.9	2504.1
$\kappa\bar{H}(t-12)$	5242.9	3393.0
$\kappa\bar{H}(t-d_A^*)$	5415.7	3176.1

Table 6.4: Exponential growth for annuals with $r = \kappa$

won't be anything for next season.

Finally, we consider an annual population where $r = \kappa$; that is, we'll take $r = 0.1$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.1$, and $b = 2$. This results in $d_A^* = 10$ and the optimal strategy of $\gamma^*(t) = \kappa\bar{H}(t - d_A^*)$ here. Although we again see that $\gamma^*(t) = \kappa\bar{H}(t - d_A^*)$ appears to be optimal, according to Table 6.4, this set of simulations featured a lot more variation in the results than the previous three. This is due to the much larger value of r compared with the other simulations, which allows for more growth to occur more rapidly. A set of simulations like this highlights the potential disadvantage if a non-optimal strategy is chosen; for example, the average yield for $\gamma(t) = \kappa\bar{H}(5 - t)$ in the following season was less than a fifth of the average yield corresponding to $\gamma(t) = \kappa\bar{H}(t - 12)$ and $\gamma^*(t)$.

Our next task is to run a few of these simulations again, but assume logistic growth instead of exponential growth. To do this, recall we simply change the stochastic DE for W_t to (6.1), where $r > 0$ is the logistic growth rate, and $K > 0$ is the carrying capacity for the population. Note that, if we assume this DE instead of (2.3), but keeping the objective function the same, then, referring to the Pontryagin Maximum

Principle (Theorem 4.4), the Hamiltonian for the system (2.2, 6.1, 2.4) will be

$$H(t, W_t, \gamma(t), p(t), q(t)) = W_t \left(r \left(1 - \frac{W_t}{K} \right) p(t) + \gamma(t)(b - p(t)) + \sigma q(t) \right),$$

where $(p(t), q(t))$ are the first-order adjoint for the system. Thus, we see that, for $\gamma(t)$ to be an optimal control under logistic growth, it, again, is either equal to 0 (if $b < p(t)$) or κ (if $b > p(t)$; we'll also, for convenience, define $\gamma(t) = \kappa$ if $b = p(t)$). So, it makes sense to try the same strategies we looked at previously; that is, strategies of the form $\gamma(t) = \kappa \bar{H}(t - d)$, where d is to be determined. However, this time, we have another parameter, K, we need to consider. Thus, we will keep all other parameters fixed and look at three different values for K (specifically, $K = 500, 1000$, and 2000) and see if varying K makes a difference in what may be an optimal strategy as well as if the logistic assumption changes what should be an optimal strategy from the exponential growth case.

We begin by using the parameter values from Table 6.1; that is, $r = 0.03$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.1$, $a = 0.8$, and $b = 2$. Recall that this resulted in $d_P \approx 7.493$. From Table 6.5, it appears that a strategy of the form $\gamma(t) = \kappa \bar{H}(t - d)$, where $d \geq 0$ is the starting time for reproduction, is again optimal. However, the starting time appears to change depending on the value of K. Specifically, when K is sufficiently low compared to W_0, season-long reproduction appears optimal, but, as K is increased, the starting time becomes later in the season ($\gamma(t) = \kappa$ is the optimal choice among those strategies tested when $K = 500$ and $K = 1000$, but $\gamma(t) = \kappa \bar{H}(t - 2)$ is the optimal choice when $K = 2000$). This certainly makes sense because, if K is low, then the population should not experience much growth (and in fact is more likely to experience decay), and our work in Section 3.4 told us that a sufficiently low growth rate will lead to season-long reproduction. On the other hand, since, in this case, $d_P > 0$, and, taking the limit of (6.1) as K approaches infinity results in (2.3), then a very large K in this case should result in more delayed reproduction. But, regardless of what K is, keeping all other parameters fixed, the overall growth is expected to be less than that of the exponential growth model, and so it makes sense that reproduction would start earlier than d_P here. The standard deviations also decrease quite a bit from what they were in the exponential case, and decrease further as K decreases. This is most likely due to the logistic growth keeping the total biomass largely in check thanks to the carrying capacity as compared to exponential growth.

We now check to see if we observe the same phenomena with annuals. So, we use the parameter values from Table 6.3; that is, $r = 0.05$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.2$, and $b = 2$. Recall that this resulted in $d_A \approx 10.758$. From Table 6.6, we notice that, as in Table 6.5, a strategy of the form $\gamma(t) = \kappa\bar{H}(t - d)$ seems to be optimal. Again, sufficiently low values of K compared to W_0 suggest season-long reproduction is optimal, and the optimal d seems to increase in value as K increases ($\gamma(t) = \kappa$ is the optimal choice among those strategies tested when $K = 500$ or $K = 1000$, but $\gamma(t) = \kappa\bar{H}(t - 5)$ is the optimal choice when $K = 2000$). However, even as K increases, d seems to stay below d_A.

Finally, we look at some multiseason simulations. Specifically, we'll consider two perennials cases, each making use of the optimal strategy $\gamma^*(t) = \kappa\bar{H}(t - d_P)$: one where the lower bound on the median of $X_1 \cdots X_n$ found in Section 5.3, F (5.5), is greater than 1, and one where it is less than 1. We'll then look at one annuals case where $d_A = 0$. Then, we'll repeat these with the same parameters, but using logistic growth instead, only varying the carrying capacity K, to see what differences there are. In this case, since Tables 6.5 and 6.6 indicate that a strategy of the form $\gamma^*(t) = \kappa\bar{H}(t-d)$ is optimal, we ran single-season simulations to estimate a value for

d for the given parameter values.

For all of these simulations, in accordance with the Central Limit Theorem, we will measure the results only after a sufficiently large number of seasons since this is what we used to obtain the lower bound on the median of $X_1 \cdots X_n$. So, we will measure the results after 100 seasons since, usually, when it comes to the Central Limit Theorem, "sufficiently large" is assumed to mean at least 30 trials, as discussed in [13, p. 309].

To begin, we consider a perennial population, taking $r = 0.05$, $\sigma = 0.05$, $T = 20$, $\kappa = 0.1$, $a = 0.8$, and $b = 2$. This results in $d_P \approx 10.6$ and $F \approx 1.293$. We then observe the following:

$$\begin{aligned} \text{Probability of Success} &= 1 \\ \text{Average Yield After 100 Seasons} &\approx 1.2457 \cdot 10^{56} \\ \text{Minimum Yield After 100 Seasons} &\approx 1.4609 \cdot 10^{52} \\ \text{Maximum Yield After 100 Seasons} &\approx 9.6034 \cdot 10^{57} \\ \text{Std. Dev. After 100 Seasons} &\approx 5.4284 \cdot 10^{56}. \end{aligned}$$

So, here, we notice that even the minimum yield after 100 seasons was a staggering amount higher than the initial amount, $W_0 = 1000$, and the standard deviation is also extremely large! Given that the lower bound on the median of $X_1 \cdots X_n$ is bigger than 1, this is not a complete surprise since this indicates that the true median is bigger than 1; however, to experience rampant growth like this seems to indicate that the true median is actually quite a bit bigger than 1. This indicates a potential problem with using $F > 1$ as a sufficient condition for likely long-term growth, and we will explore this issue further in the following simulations and in Appendix B. It is also worth noting, according to MATLAB, every multiseason trial experienced monotonic growth; that is, from season to season, growth always occurred.

Next, we take $r = 0.05$, $\sigma = 0.4$, $T = 30$, $\kappa = 0.1$, $a = 0.5$, and $b = 5$. This results in $d_P \approx 17.163$ and $F \approx 0.190$. We then observe the following:

$$\text{Probability of Success} \approx 0.22$$

$$\text{Average Yield After 100 Seasons} \approx 2.5991 \cdot 10^{16}$$

$$\text{Minimum Yield After 100 Seasons} \approx 1.7934 \cdot 10^{-26}$$

$$\text{Maximum Yield After 100 Seasons} \approx 2.5159 \cdot 10^{19}$$

$$\text{Std. Dev. After 100 Seasons} \approx 7.9571 \cdot 10^{17}$$

Here, we note that it was indeed possible for the population to not experience growth after 100 seasons, and, as the minimum yield suggests, the population may end up essentially dying out as a result. Also, in this case, according to MATLAB, none of the trials here experienced monotonic growth; that is, decay occurred at least once from season to season during each trial. This is certainly not surprising, considering the very high volatility assumed here.

Since the lower bound on the median was much less than 1, it probably doesn't seem too surprising that many of the multiseason trials did not experience growth after 100 seasons. However, to illustrate the point that, just because the lower bound is less than 1, it doesn't imply that growth is not all that likely to occur, let's run another set of simulations, taking $r = 0.03$, $\sigma = 0.2$, $T = 20$, $\kappa = 0.1$, $a = 0.5$, and

$b = 2$. This results in $d_P \approx 5.549$ and $F \approx 0.734$. We then observe the following:

$$\begin{aligned}
\text{Probability of Success} &= 1\\
\text{Average Yield After 100 Seasons} &\approx 4.6952 \cdot 10^{36}\\
\text{Minimum Yield After 100 Seasons} &\approx 1.3852 \cdot 10^{24}\\
\text{Maximum Yield After 100 Seasons} &\approx 1.6607 \cdot 10^{39}\\
\text{Std. Dev. After 100 Seasons} &\approx 6.3071 \cdot 10^{37}
\end{aligned}$$

So, even with the lower bound on the median being a fairly decent amount less than 1, growth still occurred in every multiseason trial, and the minimum yield after 100 seasons was still extremely large compared to the initial yield, $W_0 = 1000$! This numerically illustrates the fact that, if $F < 1$, we really can't predict anything about what will happen in advance. It is still quite possible growth (and large growth, at that) will occur!

As a final comment on F in this chapter, we will do one more set of simulations, this time keeping the parameter values the same as in the previous set, but taking $T = 10$ so that $d_P = 0$ and $F \approx 0.886$. We then observe the following:

$$\begin{aligned}
\text{Probability of Success} &= 1\\
\text{Average Yield After 100 Seasons} &\approx 1.1919 \cdot 10^{25}\\
\text{Minimum Yield After 100 Seasons} &\approx 5.6016 \cdot 10^{17}\\
\text{Maximum Yield After 100 Seasons} &\approx 2.4886 \cdot 10^{27}\\
\text{Std. Dev. After 100 Seasons} &\approx 9.4680 \cdot 10^{25}
\end{aligned}$$

So, although the lower bound on the median increased from the previous set of simulations, all of the statistics (except probability of success, which remained 1) decreased in comparison to the previous set. This makes sense given the way that the lower bound on the median was constructed in Section 5.3.1: if $d_P = 0$, then the lower bound on the integral of $\gamma(t)W_t$ does not need to be adjusted to use formulas from Yor. Thus, if d_P is close to 0, the lower bound on the median should be tighter. For a more detailed discussion of this lower bound on the median, refer to Appendix B.

Next, we consider an annuals population; that is, we take $r = 0.03$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.2$, and $b = 2$. This results in $d_A = 8.840$ and $F \approx 0.567$. We then observe the following:

$$\begin{aligned}\text{Probability of Success} &= 1\\ \text{Average Yield After 100 Seasons} &\approx 4.3943 \cdot 10^{43}\\ \text{Minimum Yield After 100 Seasons} &\approx 1.9876 \cdot 10^{32}\\ \text{Maximum Yield After 100 Seasons} &\approx 1.8689 \cdot 10^{46}\\ \text{Std. Dev. After 100 Seasons} &\approx 7.1680 \cdot 10^{44}\end{aligned}$$

Considering the data we obtained for the perennials cases, these results aren't too surprising. Taking both the perennials and annuals results together, however, illustrates a significant flaw in assuming exponential growth over many seasons: in every case, the average yield after 100 seasons was extremely high compared to W_0, even in the one case where growth did not occur a majority of the time.

Next, we run some multiseason simulations using some of the same parameter values, but assuming logistic growth instead and see how the results change. As previously discussed, the starting time for reproduction to be used in each case is not an exact amount; instead, it's an estimate based on MATLAB experiments with logistic simulation and assuming the optimal control is of the form $\gamma(t) = \kappa\bar{H}(t-d)$, where d is to be determined. Once again, we will also look at differences when different carrying capacities are assumed as well.

As indicated in the single-season simulations, the optimal reproduction time can change depending on the relationship between the initial biomass and K. Since a different initial biomass will be present each season in the multiseason simulations, it is expected that, for each season, the optimal reproduction time will change. However, to keep things simple, and to also afford a direct comparison with the exponential growth case, we will assume that reproduction begins at the same time each season in accordance with the optimal reproduction time from the first season.

To begin, we take the same parameter value as for the first perennial multiseason simulation with exponential growth; that is, $r = 0.05$, $\sigma = 0.05$, $T = 20$, $\kappa = 0.1$, $a = 0.8$, and $b = 2$. Table 6.7 illustrates the results. Immediately, we notice that the average yield after 100 seasons has decreased dramatically from the results we received when assuming exponential growth, and the standard deviations have also decreased dramatically, this time even lower than the initial biomass of 1000. From these results, it appears that increasing the carrying capacity does increase the average yield and also increases the standard deviation, which also happens in the single-season simulations. It is not surprising that average yield increases when the carrying capacity increases since, as the carrying capacity increases, the logistic growth becomes more and more like exponential growth. More importantly, if the population is below the carrying capacity, it is expected to grow, whereas, if the population is above the carrying capacity, it is expected to decay (the growth term will be negative).

It does seem quite strange, however, that the standard deviation decreases when going from $K = 1000$ to $K = 500$ since $K = 1000$ means the initial biomass is at the carrying capacity, and this is an equilibrium solution for the deterministic logistic model. This seems to be due to the reproduction taking place: more absolute gains from reproduction are expected when $K = 1000$ since both involve season-long reproduction, but these larger gains, combined with environmental variability and the changing growth rate (which should be changing faster due to the increased amount of growth from reproduction), should result in a higher standard deviation.

Next, we take $r = 0.03$, $\sigma = 0.2$, $T = 10$, $\kappa = 0.1$, $a = 0.5$, and $b = 2$. Table 6.8 illustrates the results. Here, we notice a few differences from Table 6.7. Since the volatility and b/a ratio were increased, it is not surprising that the end results show a lot more variability. We also notice that, when $K = 500$, it was possible to end up with runs where decay actually occurred after 100 seasons. This appears to be due to the increased volatility as well as the decreased growth rate, season length, and season-to-season survivorship in comparison to Table 6.7.

Finally, Table 6.9 illustrates results for an annual population, taking $r = 0.03$, $\sigma = 0.15$, $T = 20$, $\kappa = 0.2$, and $b = 2$ (these are the same values as in the annual multiseason simulation with exponential growth). These annuals definitely experience more dramatic growth than the perennials cases in Tables 6.7 and 6.8; this appears to be due to the higher value of κ here than in the perennial simulations (those all featured $\kappa = 0.1$). The standard deviations all go up quite a bit as well, despite the fact that σ was decreased from the previous perennials case. This appears to be due to an increased T (a longer season means more potential large effects from the environment) and an increased κ (the reproduction term in the SDE is still exponential, and a high b could mean a very high return from season-to-season).

In summary, it appears that, in the logistic case, the carrying capacity, K, as well as both κ and b/a (in the perennials case) carry significant weight in the overall multiseason behavior of the plants. Since the reproduction term in (6.1) remains an exponential term, and the objective function remains unchanged, this is not too surprising. This also explains why a population under logistic growth can still exceed its carrying capacity by quite a bit over multiple seasons, as we observed in all of the simulations. Having a higher volatility resulting in an increase in the standard deviations as well is also not surprising, especially since the environmental term also remains an exponential term in (6.1).

Remark: Clearly, the average yields obtained for a vast majority of these simulations are not practical results, as they imply extremely rapid growth. This is due to the choices of parameter values. However, the intent of this section was to illustrate the mathematical concepts, not to obtain practical results, especially since there does not appear to be an efficient way to measure some of these parameters (ex. κ and σ). So, any "practical" results we would have obtained would have been purely coincidental.

Gamma	**Avg. Value** ($K = 500$)	**Std. Dev.** ($K = 500$)
0	500.1	247.5
$\kappa\bar{H}(6-t)$	1231.8	283.8
$\kappa\bar{H}(d_P-t)$	1337.7	318.0
$\kappa\bar{H}(13-t)$	1566.2	384.4
κ from 4 to 11	1191.8	367.4
0 from d_P to 18	1417.3	349.2
κ	1731.8	458.5
$\kappa\bar{H}(t-2)$	1357.2	288.4
$\kappa\bar{H}(t-15)$	860.1	388.1
$\kappa\bar{H}(t-d_P)$	1283.9	480.7

Gamma	**Avg. Value** ($K = 1000$)	**Std. Dev.** ($K = 1000$)
0	730.5	379.7
$\kappa\bar{H}(6-t)$	1427.5	389.7
$\kappa\bar{H}(d_P-t)$	1483.2	392.6
$\kappa\bar{H}(13-t)$	1800.3	499.0
κ from 4 to 11	1486.6	524.8
0 from d_P to 18	1660.7	495.3
κ	2002.8	589.2
$\kappa\bar{H}(t-2)$	1997.1	511.2
$\kappa\bar{H}(t-15)$	1207.0	617.2
$\kappa\bar{H}(t-d_P)$	1657.7	691.8

Gamma	**Avg. Value** ($K = 2000$)	**Std. Dev.** ($K = 2000$)
0	988.1	569.4
$\kappa\bar{H}(6-t)$	1529.7	479.4
$\kappa\bar{H}(d_P-t)$	1638.2	481.3
$\kappa\bar{H}(13-t)$	1958.3	625.8
κ from 4 to 11	1694.6	685.3
0 from d_P to 18	1791.3	624.1
κ	2139.8	700.7
$\kappa\bar{H}(t-2)$	2711.5	814.4
$\kappa\bar{H}(t-15)$	1554.3	827.8
$\kappa\bar{H}(t-d_P)$	1995.5	940.7

Table 6.5: Logistic growth for perennials without season-long reproduction

Gamma	**Avg. Value** ($K = 500$)	**Std. Dev.** ($K = 500$)
$\kappa\bar{H}(5-t)$	1204.7	186.1
$\kappa\bar{H}(d_A-t)$	1700.9	325.4
$\kappa\bar{H}(12-t)$	1767.7	337.5
κ from 5 to 15	1375.7	411.7
0 from d_A to 18	1812.8	359.1
κ	1928.7	370.9
$\kappa\bar{H}(t-5)$	1553.8	482.5
$\kappa\bar{H}(t-12)$	1055.4	386.4
$\kappa\bar{H}(t-d_A)$	1133.1	397.3

Gamma	**Avg. Value** ($K = 1000$)	**Std. Dev.** ($K = 1000$)
$\kappa\bar{H}(5-t)$	1293.4	204.7
$\kappa\bar{H}(d_A-t)$	1878.1	400.1
$\kappa\bar{H}(12-t)$	1953.5	396.9
κ from 5 to 15	1829.8	597.0
0 from d_A to 18	2012.8	438.5
κ	2193.4	508.0
$\kappa\bar{H}(t-5)$	2034.3	700.4
$\kappa\bar{H}(t-12)$	1563.9	664.7
$\kappa\bar{H}(t-d_A)$	1686.0	692.3

Gamma	**Avg. Value** ($K = 2000$)	**Std. Dev.** ($K = 2000$)
$\kappa\bar{H}(5-t)$	1345.8	235.3
$\kappa\bar{H}(d_A-t)$	1997.5	444.4
$\kappa\bar{H}(12-t)$	2061.6	487.3
κ from 5 to 15	2174.0	814.9
0 from d_A to 18	2154.4	498.7
κ	2311.4	544.1
$\kappa\bar{H}(t-5)$	2484.5	971.8
$\kappa\bar{H}(t-12)$	2149.5	992.1
$\kappa\bar{H}(t-d_A)$	2267.7	1009.9

Table 6.6: Logistic growth for annuals with $r \neq \kappa$

	$K = 500 (d \approx 0)$	$K = 1000 (d \approx 0)$	$K = 2000 (d \approx 2)$
Success Prob.	1	1	1
Avg. End Yield	3603.8	7227.7	9789.0
Min. End Yield	2863.3	5776.9	7337.8
Max. End Yield	4366.1	9000.0	13585.0
Std. Dev.	223.0	469.8	796.7

Table 6.7: Logistic growth for perennials over multiple seasons without season-long reproduction

	$K = 500 (d \approx 0)$	$K = 1000 (d \approx 0)$	$K = 2000 (d \approx 0)$
Success Prob.	0.991	1	1
Avg. End Yield	2848.8	5665.3	11595.0
Min. End Yield	714.2	1295.7	2453.0
Max. End Yield	7372.6	15608.0	25574.0
Std. Dev.	928.1	1919.9	3669.0

Table 6.8: Logistic growth for perennials over multiple seasons with season-long reproduction

	$K = 500 (d \approx 0)$	$K = 1000 (d \approx 0)$	$K = 2000 (d \approx 5)$
Success Prob.	1	1	1
Avg. End Yield	9414.3	18701.0	37688.0
Min. End Yield	5316.5	10831.0	20947.0
Max. End Yield	15177.0	28207.0	57902.0
Std. Dev.	1473.3	2825.8	5645.1

Table 6.9: Logistic growth for annuals over multiple seasons

Chapter 7

Conclusion

In this work, we have attempted to provide an answer to Lamont Cole's famous paradox about what conditions would lead to annual plants dominating over perennials in a region. To do so, we required that both would be reproducing optimally in the sense that they would be allocating energy during the season in a fashion that would maximize their expected yield (in terms of adult biomass) for the following season. Evolutionary forces dictate that the species that reproduces optimally should dominate those that reproduce suboptimally.

Creating a model which incorporated both fixed, deterministic parameters as well as environmental stochasticity, we showed, in Chapters 3 and 4, that the optimal reproduction strategy for both annuals and perennials is either to reproduce all season long, or to begin the season not reproducing at all and then waiting until a time completely determined by the deterministic parameters to begin reproduction. In either case, when reproduction takes place, the plants devote as much energy as they are able to reproduction until the end of the season. Season-long reproduction, as we showed in Section 3.4, became the optimal strategy when the season was sufficiently short and/or the growth rate was sufficiently small. Other parameters could play a role as well, but these were found to be the two dominant parameters in this case.

Once this optimal strategy was established, we assumed that the plants would follow this strategy every season. Then, assuming each season's parameters were the same, and each season's dynamics were independent of all others, we attempted to answer Cole's question in Chapter 5, with some numerical data in Chapter 6. Overall, we found that annuals are expected to dominate over perennials if one or more of the following conditions are true:

- The environmental volatility is sufficiently high.
- The reproductive utility factor is sufficiently high.
- The intrinsic growth rate is sufficiently small.
- The maximum proportion to be devoted to reproduction at any instant is sufficiently high.
- The season is sufficiently long.
- The season-to-season survivorship of adult perennials is sufficiently low, pending one or more of the previous conditions are met.

Many of these conclusions are supported by prior work; for example, Young's model in [29] also showed that low survivorship of adult perennials was a generally favorable condition for annuals. In [4], Clary studied grass populations in the Iberian Peninsula, which, although was historically dominated by perennial grasses, has since become dominated by annuals in certain areas. In the areas where annuals dominated, he found the two driving forces seem to be annual rainfall (summer droughts favored annuals) and disturbance from grazing. This seems to support the conclusion concerning environmental volatility. A similar result was derived by Iwasa and Cohen in [14], who found that lower habitat reliability favored annuals. Garnier ([11]) also cited results saying that unpredictability of the environment favored annuals. However, the main content of [11] is a study of seven types of grass of the same subfamily, *Pooideae*, each type consisting of an annual and perennial species (six pairs were of the same genus). In doing so, Garnier discovered that the corresponding annual species always had a higher relative growth rate than the perennial species. Although this is not a confirmation that annuals are favored when the intrinsic growth rate is sufficiently small, it does lend credence to the observation that, for high growth rates, perennials seem to dominate over annuals. So, to keep pace, it is justifiable that annuals would need higher growth rates than their perennial counterparts. On the other hand, Young ([29]) argues that a higher growth rate favors annuals, not perennials. The climate in the regions studied by Clary in [4] are characterized by hot, dry summers and mild, wet winters, and so the growing season in this region is fairly long compared to, say, in interior Canada. However, as Clary explained, there are regions he studied where perennials still dominate, so this does contradict our conclusion that a long growing season tends to favor annuals. Iwasa and Cohen ([14]) discuss that a shorter season should favor annuals, which contradicts our conclusion that a shorter season would favor perennials. Our contradictions with Young and Iwasa/Cohen seem to be due to the different sets of assumptions that were used to construct these models and ours; nevertheless, our results should be investigated further.

We now turn our attention to the reasonability of the model used in this work. Two key issues about the model are issues that may need to be addressed in future work; namely, using exponential growth as opposed to something more density-dependent, like logistic growth (used partially in Chapter 6), and the environmental stochasticity term. Using exponential growth, especially over multiple seasons like was done in

Chapters 5 and 6, will, of course, lead to unrealistic results since resources are limited, and perennials cannot continue growing at such a fast rate indefinitely. Exponential growth may be justifiable, however, for a single-season model, especially for small plants or plants in early stages of life in a uniform environment ([26, p. 76, 81]). It was chosen in this work mainly due to the ability to solve the corresponding SDE exactly, which we did in Chapter 4.

Of course, logistic growth is a more realistic assumption, since it takes resource availability into account, assuming there is a finite supply of resources ([26, p. 86]). However, as of this work, no one has been able to write down an analytic solution for the logistic SDE, which makes finding an optimal control extremely difficult since we would be essentially forced to do so numerically. But, some potential promise in this model is that numerical simulations (Chapter 6) seemed to indicate that an optimal control is of the same form as when exponential growth is assumed; writing the Hamiltonian in this case indicated a "bang-bang" optimal strategy as well. So, we may be able to derive an optimal control for the deterministic model and then attempt to prove (though not the same way as in Chapter 4 since we can't solve it analytically) that the control is still optimal when stochasticity is introduced. Thus, incorporating logistic growth is certainly something that will be done in the future.

The way that environmental stochasticity is incorporated into the model is also a key issue, since, although randomness certainly exists in the environment, the environment is not completely random. For example, it is known in Nebraska that, during July and August, days where the high temperature is 90 degrees or more are common, but are very rare in, say, May. Rainfall also has an element of predictability: many regions typically have a "dry season" and a "wet season," for example. Thus, it may be more accurate to make the environmental term a sum of a deterministic piece and a random piece. One potential idea is to use a cosine function for temperature, since average temperature increases at the start of a growing season, peaks somewhere in the middle, and then decreases afterward. This could make the model extremely difficult to solve, however, and many environmental effects (such as disease, which would not be as predictable) would be left out, which is why it wasn't done here.

Another issue with the model is measuring the parameters in practice. Some of the parameters may not be too difficult to measure (T is just the length of the growing season), but others may be extremely difficult. The two most difficult parameters to measure appear to be κ and σ. It does appear that some work has been done with trying to measure reproductive allocation (see, for example, [2]), however, so this may be a tractable problem. To measure σ, it appears that, first, one would have to measure r and then try to see what deviations from r tend to be in the environment in order to measure σ. This appears to be very time-consuming since it seems to require field measurements over many years as well as measurements in a more controlled setting for comparison. Thus, use of the model in practical situations may not be possible until efficient ways to measure all of the parameters exist.

One other issue is the multiseason analysis done in Chapter 5. Although, mathematically, there is nothing wrong with what was done, the sufficient condition for growth that was derived is extremely weak (this is explored further in Appendix B), especially since it only guarantees growth at least 50% of the time, saying nothing of how much growth can be reasonably expected. One thing to be done in the near future is to attempt to turn the lower bound on the median into a tighter bound, and maybe find the median exactly. This will also serve as a check of the conditions for annual dominance stated previously. Preferably, a stronger condition which will also provide an idea of how much growth can be reasonably expected, can be derived. Regardless of whether this can be done or not, none of the analysis in that chapter will work for logistic growth, and, if the SDE can't be analytically solved, numerical work may be the only way to proceed with multiseason analysis for logistic growth.

Besides looking at logistic growth, another way to extend the model would be to break the plants into two parts; namely, the vegetative, or non-reproductive part, and the reproductive part, known as a “root-shoot” model. Each part can be assessed its own environmental stochasticity (the parts underground could be considered “safer” than those above ground, for example), and the objective function can be tweaked to account for different season-to-season survivorships for each portion of the plant.

A basic model for this is given in [20, p. 1]; specifically, taking $u(t)$ to be the control function, $x_1(t)$ to be the biomass in the vegetative part at time t, and $x_2(t)$ to be the biomass in the reproductive part at time t, the constraints are given as follows:

$$\begin{aligned}\frac{dx_1}{dt} &= u(t)x_1\\ \frac{dx_2}{dt} &= (1-u(t))x_2(t).\end{aligned}$$

Here, we assume $0 \leq t \leq T$ and $0 \leq u(t) \leq 1$ for all t. Thus, the changes necessary for this to fit our model would be relatively straightforward, and, if we continue to assume exponential growth, the model may still be solvable. This will be investigated in the future as well.

Appendix A

MATLAB Routines

This appendix contains the two MATLAB routines which were used to conduct the simulations in Chapter 6 and Appendix B, along with some brief commentary on some of the commands.

The first routine, "ecosim," is a program which, given parameter values, computes the value of the objective function (2.2) after a single season. It was used in Chapter 6 to verify that the optimal controls we found in Chapter 4 were indeed optimal and to compute some statistics when logistic growth is assumed. The routine is as follows:

```
function ecosim

clear all

randn('state',sum(100*clock));
    %sets up the random number generator
    %(without this, MATLAB picks the exact same values
    %when using randn every time the program is restarted)
```

```
p=1000;
    %number of single-season runs
n=1000;
    %number of measurement periods (steps) in season
T=20;
    %length of season
k=0.1;
    %kappa; max proportion of biomass that can be
    %invested for reproduction
r=0.03;
    %growth rate in absence of environmental effects
a=0.8;
    %survivorship of adult biomass from one season to next
b=2;
    %proportionality between adult biomass
    %and next season potential
sigma=0.15;
    %volatility of environment (standard deviation for
    %the random normal distribution we'll be drawing from)

success=0;
    %counter for number of runs where growth occurs
C=zeros(n+1,p);
    %matrix of adult biomasses for each sim
D=zeros(n,p);
    %matrix of juvenile biomasses for each sim
```

```
H=zeros(p,1);

    %vector of populations at end of generation

N=zeros(p,1);

    %vector of no. of steps no reproduction took place


for m=1:p

B=zeros(n+1,3);

    %initialize the matrix of data; the first column will

    %be the dBt chosen for that period, the second will be

    %the amount of new (juvenile) biomass

    %produced in that time period, and the third will be

    %the amount of adult biomass at the end

    %of the time period

B(1,3)=1000;

    %initial adult biomass

norep=0;

    %counter for how many steps reproduction did not occur

for j=2:n+1

    brownian=sqrt(T/n)*randn;

            %approximation of B(t_j)-B(t_(j-1))

    B(j,1)=sigma*brownian;

    if (j-1)*(T/n) >= T - (1/(r-k))*log(b*r/(a*(r-k)+b*k))

        gamma=k;

            %control function gamma

    else gamma=0;

        norep=norep+1;
```

```
    end
    B(j,2)=gamma*(T/n)*B(j-1,3);
            %what has been allocated for reproduction
    if B(j-1,3)>=0;
        B(j,3)=B(j-1,3)*(1+r*(T/n)-gamma*(T/n)+B(j,1)
                +(1/2)*sigma^2*(brownian^2-(T/n)));
    else B(j,3)=0;
    end
    if B(j,3)<=0;
        B(j,3)=0;
            %this is to ensure the population is never negative
    else B(j,3)=B(j,3);
    end
end
C(:,m)=B(:,3);
    %amount of adult biomass at end of season
D=b*sum(B(2:n+1,2));
    %total new adult biomass for next season
H(m,1)=D+a*C(n+1,m);
    %total adult biomass for next season
if D+a*C(n+1,m)>=B(1,3);
    success=success+1;
end
N(m,1)=norep*(T/n);
end
```

```
avgsuccess=success/p
    %proportion of successes
avgnorep=mean(N)
    %average # of times no reproduction occured for each run
mendpop=min(H)
    %minimum yield for next season of the p runs
Mendpop=max(H)
    %maximum yield for next season of the p runs
avgendpop=mean(H)
    %average yield for next season of the p runs
stdevendpop=std(H)
    %standard deviation of the yield for next season
medianendpop=median(H)
    %median yield for next season of the p runs
```

We make a few comments on the program. First, if one wants to consider logistic growth instead of exponential, simply add in a value for K, the carrying capacity, in the beginning with the rest of the parameters, and, in the line where the value for $B(j,3)$ is being set, change $r*(T/n)$ to $r*(1-B(j-1,3)/K)*(T/n)$ since the logistic growth piece in the SDE (see Chapter 6) is $rW_t(1-W_t/K)$ as opposed to the exponential growth piece rW_t.

Next, although the optimal starting time for reproduction is given as the point where γ switches values from 0 to κ in the program, it can easily be changed to be any value the user wishes (for example, if one wants $\gamma(t) = \kappa\bar{H}(t-2)$, simply take $(j-1)*(T/n) >= 2)$, or the inequality can be flipped (for example, if one wants

$\gamma(t) = \kappa\bar{H}(d_P - t))$. The $(j-1)$ factor is present to ensure that the reproduction actually begins at the given starting time.

The most important line in this program is the line

```
B(j,3)=B(j-1,3)*(1+r*(T/n)-gamma*(T/n)+B(j,1)
                      +(1/2)*sigma^2*(brownian^2-(T/n))),
```

since this line allows us to approximate a sample path that serves as a solution to the SDE. The method being used here is Milstein's method; specifically, if we are trying to approximate the solution to the SDE

$$dX(t) = f(X(t))dt + g(X(t))dB(t),$$

where X_0 is given, $t \in [0,T]$, and f, g are functions which are "nice" enough to guarantee a unique solution (see Theorem 4.2), then, if h is the step size (so, there are T/h steps overall), we can approximate the solution to this SDE by the following:

$$X_{j+1} = X_j + hf(X_j) + g(X_j)(B_{t_{j+1}} - B_{t_j}) + (1/2)g(X_j)g'(X_j)\left((B_{t_{j+1}} - B_{t_j})^2 - h\right)$$

for $j = 0, 1, \ldots, (T/h) - 1$. Since, for our model, $f(W_t) = (r - \gamma(t))W_t$ and $g(W_t) = \sigma W_t$, then choosing a step size of T/n gives us the above line.

We will omit a theoretical discussion of Milstein's method save for the fact that it is strongly convergent with order 1; that is, there exists a constant C such that

$$E\left[X_n - X(t_n)\right] \leq Ch$$

for any fixed $t_n = n(T/h)$ and h sufficiently small. In contrast, the Euler-Maruyama method, the stochastic analog of Euler's method from ordinary differential equations, is strongly convergent with order 1/2; that is, the right-hand side of the above inequality becomes $Ch^{1/2}$. The difference between Euler-Maruyama and Milstein is simply the deletion of

$$(1/2)g(X_j)g'(X_j)\left((B_{t_{j+1}} - B_{t_j})^2 - h\right).$$

The reader who is interested in more information on Euler-Maruyama and Milstein's methods may consult [12].

The next routine, "multiseason," is a program which essentially takes the "ecosim" program and duplicates it for multiple seasons; that is, the total amount of adult biomass that will be present at the beginning of next season is used as the new initial value, and then "ecosim" is run again. It was used in Chapter 6 to compute multiseason statistics for both exponential and logistic growth. The routine is as follows; note that many of the commands are exactly the same as in "ecosim," so all comments are omitted except for those on new commands:

```
function multiseason


clear all


randn('state',sum(100*clock));


r=1000;
     %number of multiseason runs
N=100;
     %number of seasons per run
```

```
n=1000;

T=20;

k=0.2;

r=0.03;

a=0;

b=2;

sigma=0.15;


nomonotone=0;

     %counter for tracking if pop is NOT

     %monotone increasing over entire run

growth=0;

     %counter for tracking if pop grows at end of each run

P=zeros(r,1);

     %vector of biomass at end of each run

for p=1:r

    A=zeros(N+1,1);

         %vector of biomass at start of each season

    A(1,1)=1000;

         %initial adult biomass

    for m=1:N

    B=zeros(n+1,3);

    B(1,3)=A(m,1);

         %initial adult biomass at start of season

    C=zeros(n,1);

    for j=2:n+1
```

```
    brownian=sqrt(T/n)*randn;
    B(j,1)=sigma*brownian;
    if (j-1)*(T/n) >= T - (1/(r-k))*log(b*r/(a*(r-k)+b*k))
        gamma=k;
    else gamma=0;
    end
    B(j,2)=b*gamma*(T/n)*B(j-1,3);
    if B(j-1,3)>=0;
        B(j,3)=B(j-1,3)*(1+r*(T/n)-gamma*(T/n)+B(j,1)
                +(1/2)*sigma^2*(brownian^2-(T/n)));
    else B(j,3)=0;
    end
    if B(j,3)<=0;
        B(j,3)=0;
    end
    end
    D=sum(B(2:n+1,2));
    A(m+1,1)=a*B(n+1,3)+D;
         %total adult biomass for next season
end
for q=1:N
if A(q,1)>A(q+1,1)
    nomonotone=nomonotone+1;
         %if decay occurs between two seasons,
         %then there is no monotone growth
    break
```

```
end
end
P(p,1)=A(N+1,1);
        %total adult biomass to start the (N+1)st season
if P(p,1)>=A(1,1)
growth=growth+1;
end
end

noincrease=nomonotone/r
     %proportion of runs that were not monotone increasing
success=growth/r
     %proportion of runs that experienced growth
minendbiomass=min(P)
     %minimum end biomass over the r runs
maxendbiomass=max(P)
     %maximum end biomass over the r runs
avgendbiomass=mean(P)
     %average end biomass over the r runs
stdevendbiomass=std(P)
     %standard deviation of the end biomass
```

Given the “ecosim” routine, this routine is pretty self-explanatory. The only comment that needs to be made is that this routine can take quite a while to run, especially if one considers a large number of seasons, a pretty small step size, and a large number of runs. Otherwise, all of the comments made for the “ecosim” routine can be applied to this routine as well.

Appendix B

Error Analysis on the Median of $X_1 \cdots X_n$

In Chapter 6, the multiseason analysis seemed to indicate a major problem with using the lower bound on the median of $X_1 \cdots X_n$ computed in Chapter 5, where

$$\begin{aligned} X_n = a \cdot \exp&\left(\left(r - \frac{1}{2}\sigma^2\right) T + \kappa(T - d_P) + \sigma B_T\right) \\ &+ b\kappa \int_{d_P}^{T} \exp\left(\left(r - \frac{1}{2}\sigma^2\right) s - \kappa(s - d_P) + \sigma B_s\right) ds, \end{aligned}$$

and $X_1, X_2, \ldots$ are independent and identically distributed, to try and get an idea of what should happen to the plants over multiple seasons. In Chapter 5, we showed that, so long as the lower bound on the median, F (5.5), was greater than 1, then the true median also had to be greater than 1, meaning that there was at least a 50% chance for the plants to experience growth over a sufficiently large number of seasons. However, even when $F < 1$, growth could still be quite rampant; one particular perennial multiseason simulation, taking $r = 0.03$, $\sigma = 0.2$, $T = 20$, $\kappa = 0.1$, $a = 0.5$, and $b = 2$ illustrated a case where $F < 1$ (in fact, $F \approx 0.734$), y et not only did the plants always experience long-term growth, but the long-term growth was always huge (on the order of at least 10^{21} times the initial biomass!).

Thus, our goal in this appendix is to investigate how far off the lower bound on the median is from the true median, which will be estimated using the "ecosim" routine described in Appendix A. What follows are the three sets of parameters used to generate Tables 6.1-6.3, two sets used for multiseason analysis, and one additional set. We first compute F (refer to Section 5.3.2, (5.5) for the formula for F) for the given set of parameters and then run "ecosim" to attempt to estimate the true median. Recall that, although we are investigating the lower bound on the median of $X_1 \cdots X_n$, we showed that, for this lower bound to be greater than 1, we only need the lower bound on the median of X_n to be greater than 1. This is why we are using "ecosim," since we only need to worry about single-season dynamics.

The parameters we will be using in each comparison are as follows:

$$\begin{aligned}
\text{Table 6.1} &: r = 0.03, \sigma = 0.15, T = 20, \kappa = 0.1, a = 0.8, b = 2 \\
\text{Table 6.2} &: r = 0.03, \sigma = 0.15, T = 12, \kappa = 0.1, a = 0.8, b = 2 \\
\text{Table 6.3} &: r = 0.05, \sigma = 0.15, T = 20, \kappa = 0.2, a = 0, b = 2 \\
\text{Multiseason 1} &: r = 0.05, \sigma = 0.05, T = 20, \kappa = 0.1, a = 0.8, b = 2 \\
\text{Multiseason 2} &: r = 0.05, \sigma = 0.4, T = 30, \kappa = 0.1, a = 0.5, b = 5 \\
\text{New Set} &: r = 0.02, \sigma = 0.1, T = 10, \kappa = 0.2, a = 0, b = 1.
\end{aligned}$$

Table B.1 illustrates the comparisons, listing the starting times for reproduction (d) in each case, since this played a significant role in constructing F, the values of F in each case, and the estimated true medians in each case. So, the table suggests that F, while it is certainly a valid lower bound, is an extremely terrible lower bound;

Data Set	d	F	**"True" Median**	**% Error**
Table 6.1	7.493 (20)	0.832	2.221	62.5%
Table 6.2	0 (12)	0.939	1.837	48.9%
Table 6.3	10.758 (20)	0.774	2.965	73.9%
Multiseason 1	10.6 (20)	1.293	3.346	61.4%
Multiseason 2	17.163 (30)	0.190	2.025	90.6%
New Set	0 (10)	0.382	0.917	58.3%

Table B.1: Error analysis on median lower bound, F

the relative error in each case is huge. Surprisingly, even though the "New Set" of data was an annual set which had $d_A = 0$, meaning we did not have to factor in an estimate for the product of two random variables nor did we have to adjust the lower bound on the integrand to match Yor's formula (see Section 5.2.1), the lower bound is still quite far off from the "true" median. However, it was the only set of parameters where F was less than 1 and so was the "true" median. In fact, in that case, "multiseason" was run just to see what would happen, and, not only did none of the runs experience growth, but the maximum biomass after 100 seasons was only about 19 units after starting with 1000.

Noting that the "true" medians for both multiseason sets of parameters were much higher than 1, it is now not surprising at all that both of those runs experienced rampant growth over the 100 seasons; after all, if it is likely that the population will at least double in biomass at the end of each season, then, after 100 seasons, the biomass will likely increase by a factor of $2^{100} \approx 10^{30}$! This then tells us that, although F does provide for a nice theoretical lower bound, it is a terrible lower bound to use in practice to try and estimate what will happen to the population over a large number of seasons. Its only real use is when $F > 1$, since this guarantees that the true median is also greater than 1.

Bibliography

[1] Ed Allen. *Modeling with Ito Stochastic Differential Equations.* Springer, The Netherlands, 2007.

[2] Caroline Brophy, D. J. Gibson, P. M. Wayne, and J. Connolly. A modelling framework for analysing the reproductive output of individual plants grown in monoculture. *Ecological Modelling*, 207:99–108, October 2007.

[3] Eric Charnoff and William Schaffer. Life history consequences of natural selection: Cole's result revisited. *The American Naturalist*, 107(958):791–793, 1973.

[4] Jeffrey Clary. Rainfall seasonality determines annual/perennial grass balance in vegetation of Mediterranean Iberian. *Plant Ecology*, 195(1):13–20, March 2008.

[5] Lamont Cole. The population consequences of life history phenomena. *The Quarterly Review of Biology*, 29(2):103–137, June 1954.

[6] R. M. Corless, G. H. Gonnet, D. E. G. Hare, D. J. Jeffrey, and D. E. Knuth. On the Lambert W function. *Advances in Computational Mathematics*, 5:329–359, 1996.

[7] Min Dai, Yue Kuen Kwok, and Jianping Zong. Guaranteed minimum withdrawal benefit in variable annuities, February 2007. Available at Social Science Research Network (SSRN): http://ssrn.com/abstract=964083.

[8] P.M. Datson, B. G. Murray, and K. E. Steiner. Climate and the evolution of annual/perennial life histories in *nemesia*. *Plant Systematics and Evolution*, 270:39–57, January 2008.

[9] Kenneth Davidson and Allan Donsig. *Real Analysis With Real Applications*. Prentice-Hall, Upper Saddle River, NJ, 2002.

[10] Gerald Folland. *Real Analysis*. John Wiley and Sons, Hoboken, NJ, second edition, 1999.

[11] E. Garnier. Growth analysis of congeneric annual and perennial plant species. *Journal of Ecology*, 80(4):665–675, December 1992.

[12] Desmond Higham. An algorithmic introduction to numerical simulation of stochastic differential equations. *SIAM Review*, 43(3):525–546, 2001.

[13] Robert Hogg and Elliot Tanis. *Probability and Statistical Inference*. Prentice-Hall, Upper Saddle River, NJ, sixth edition, 2001.

[14] Yoh Iwasa and Dan Cohen. Optimal growth schedule of a perennial plant. *The American Naturalist*, 133(4):480–505, April 1989.

[15] Yoh Iwasa and Takuya Kubo. Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology*, 11:41–65, 1997.

[16] Robert Jarrow and Philip Protter. A short history of stochastic integration and mathematical finance: the early years, 1880-1970. In *A Festschrift for Herman Rubin: Lecture Notes-Monograph Series*, volume 45, pages 75–91, 2004.

[17] Norman Johnson and Samuel Kotz. *Distributions in Statistics: Continuous Univariate Distributions 1*. John Wiley and Sons, New York, NY, 1970.

[18] Walter Kelley and Allan Peterson. *The Theory of Differential Equations*. Pearson Education, Upper Saddle River, NJ, 2004.

[19] Russell Lande. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, 142(6):911–927, December 1993.

[20] Suzanne Lenhart and John Workman. *Optimal Control Applied to Biological Models*. Chapman and Hall/CRC Press, Boca Raton, FL, 2007.

[21] R. M. Nisbet, E. B. Muller, K. Lika, and S. Kooijman. From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, 69(6):913–926, December 2000.

[22] Bernt Oksendal. *Stochastic Differential Equations*. Springer-Verlag, New York, NY, fourth edition, 1995.

[23] Shige Peng. A general stochastic maximum principle for optimal control problems. *SIAM Journal on Control and Optimization*, 28(4):966–979, July 1990.

[24] Lev Pontryagin. *The Mathematical Theory of Optimal Processes*, volume 4. Interscience, 1962.

[25] James Stewart. *Calculus: Concepts and Contexts*. Brooks/Cole, Pacific Grove, CA, second edition, 2001.

[26] John Thornley and Ian Johnson. *Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology*. The Blackburn Press, Caldwell, NJ, 2000.

[27] Jiongmin Yong and Xun Yu Zhou. *Stochastic Controls: Hamiltonian Systems and HJB Equations*. Springer-Verlag, New York, NY, 1999.

[28] Marc Yor. On some exponential functionals of brownian motion. *Advances in Applied Probability*, 24(3):509–531, September 1992.

[29] Truman Young. A general model of comparative fecundity for semelparous and iteroparous life histories. *The American Naturalist*, 118(1):27–36, January 1981.

[30] Truman Young. Evolution of semelparity in Mount Kenya lobelias. *Evolutionary Ecology*, 4(2):157–171, April 1990.