Optimal Seasonal Plant Reproductive Strategies (Take 2)

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An Opening Quote

"...[F]or the sake of brevity and to avoid cumbersome expressions, variables are omitted and assumptions made in the mathematical analysis which are not justified by the biological data."

- W.C. Allee, *Recent Studies in Mass Physiology* (1934)

Introduction

- Consider a (local) population of plants with some initial adult biomass at the start of a season
- During season, adult biomass may grow or decay depending on the environment (and the plants' intrinsic growth rate)
- Goal: choose a strategy of energy allocation to reproduction to make expected adult biomass size for next season as large as possible
- Modeled by a stochastic optimization problem, which is solved by using the stochastic *Pontryagin Maximum Principle*

Modeling Assumptions

Define the following parameters/variables (all are assumed ≥ 0):

T = length of season

W_t = adult biomass at time t

r = growth rate in absence of environmental effects

σ = volatility of environment

ϵ = average survivorship probability of juveniles to adulthood

a = average proportion of adult biomass surviving from one season to the next

u = average number of times more biomass an adult has than a seed

$\gamma(t)$ = proportion of adult biomass used for reproduction at time t

Modeling Assumptions

- The size of the adult biomass follows a Geometric Brownian Motion; that is, calling B_t Standard Brownian Motion at time t,

$$dW_t = rW_t dt + \sigma W_t dB_t$$

- The population follows an energy budget model very similar to the κ rule (Nisbet et al)
  At any time t, at most κ of the available biomass can be used for reproduction
  The remaining biomass is used for growth/somatic maintenance

The Model

The model for a season can be stated as a stochastic optimization problem as follows:

Maximize

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

subject to

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

$$W_0 = \text{constant} > 0$$

From now on, we will define $b = \epsilon u$.

The 1-D Stochastic Pontryagin Maximum Principle

Consider, for $(t, x) \in [0, T] \times G$, where $G \subseteq \mathbb{R}$, the optimization problem:

Maximize

$$E[K(W_T) + \int_0^T F(t, W_t, \gamma(t))dt]$$

subject to

$$dW_t = c(t, W_t, \gamma(t))dt + \sigma(t, W_t, \gamma(t))dB_t$$

We will also assume that $\gamma(t) \in M$, where M is the set of all measurable Markov controls that take on values in the Borel set U, where U is convex with nonempty interior (a *convex body*).

The 1-D Stochastic Pontryagin Maximum Principle

Define the (first-order) adjoint equation to be the following:

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

Under reasonable continuity and differentiability assumptions of the relevant functions (which this model has), then the solution $(p(t), q(t))$ is unique.

The 1-D Stochastic Pontryagin Maximum Principle

Assume $\sigma(t, W_t, \gamma(t)) = \sigma(t, W_t)$ (that is, σ does not explicitly depend on the control) and $W_t \in G$ for all $t \in [0, T]$ and $\gamma(t) \in M$.

If $\gamma^*(t)$ is an optimal control with corresponding trajectory W_t^* and adjoint $(p^*(t), q^*(t))$, then the following condition holds:

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

where

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

This is a necessary condition for optimality, but it can be made sufficient under additional conditions.

Applying the Maximum Principle

For our model, we have that $G = [0, \infty)$ and $U = [0, \kappa]$

Our Hamiltonian is as follows:

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

From this, it is clear that an optimal $\gamma(t)$ can then only take on two values: 0 (when $b < p(t)$) and κ (when $b \geq p(t)$).

Solution of Optimization Problem: Case 1

Assume that $a > 0$ (perennials) and $b/a \leq 1$.

It can be shown that, in this case, an optimal choice for $\gamma(t)$ is $\gamma(t) = 0$ with corresponding optimal value

$$aW_0 \cdot \exp(rT)$$

This says that, if $b/a \leq 1$, then the population is best served by focusing on preserving and growing the existing adult biomass.

Solution of Problem: Case 2

For the case $a > 0$, $b/a > 1$, and $r \neq \kappa$, it can be shown that

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

where

$$\bar{H}(y) = \begin{cases} 0, & y < 0 \\ 1, & y \geq 0 \end{cases}$$

and

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

is an optimal choice for $\gamma(t)$. (If $d_P < 0$, we just take $d_P = 0$).

Solution of Problem: Case 2

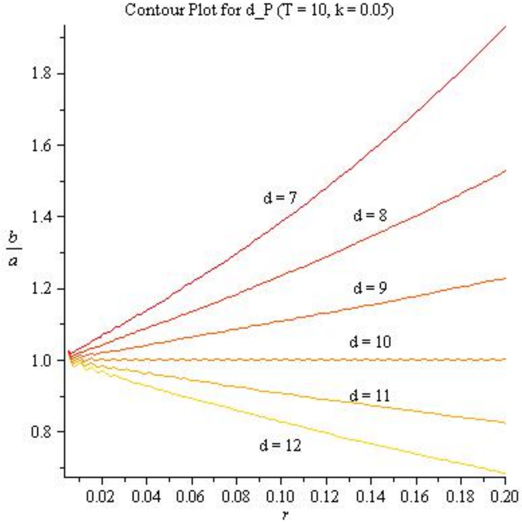
The corresponding optimal value is

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

So, if $b/a > 1$, the optimal strategy is either for the population to grow for a while and then, near the end of the season, pour all available biomass into reproduction, or reproduce all season long.

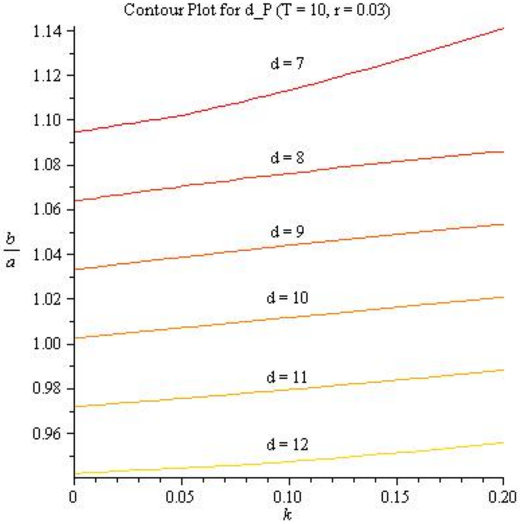
Contour Plot of d_P

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



Contour Plot of d_P

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



Numerical Data (MATLAB)

$r = 0.03,\ \sigma = 0.15,\ T = 20,\ \kappa = 0.2,\ a = 0.8,\ b = 2,\ W_0 = 1000$
$d_P \approx 11.285$

Gamma	**Value**	**Std. Dev**
0	1443.4	1040.4
$\kappa H(8-t)$	2079.9	525.9
$\kappa H(d_P-t)$	2184.9	562.4
κ from 7 to d_P	2314.5	632.4
0 from d_P to 18	1444.3	1043.4
κ	2315.4	632.9
$\kappa H(t-10)$	2807.1	1497.0
$\kappa H(t-16)$	2712.9	1772.6
$\kappa H(t-d_P)$	2854.1	1645.6

Solution of Problem: Case 3 and Special Cases

It can be shown that, if $a = 0$ (annuals) and $r \neq \kappa$, then an optimal strategy is $\gamma(t) = \kappa(\bar{H}(t - d_A))$, where

$$d_A = T - \frac{1}{r - \kappa} \ln \left(\frac{r}{\kappa} \right)$$

and the corresponding optimal value is

$$\frac{bW_0\kappa}{r - \kappa} \left(\exp(rT - \kappa(T - d_A)) - \exp(rd_A) \right)$$

If $r = \kappa$, then it can be shown that the starting time for reproduction becomes $d_P' = T - \frac{(b/a)-1}{(b/a)\kappa}$ or $d_A' = T - \frac{1}{\kappa}$ for the respective perennial and annual cases.

Multiseason Analysis

Define the following stochastic processes:

$$
\begin{aligned}
W_t^{(n)} &= W_0^{(n-1)} \exp\left(\left(r - \frac{1}{2}\sigma^2\right) t - \int_0^t \gamma^*(s) ds + \sigma B_t\right) \\
&= W_0^{(n-1)} Y_t^{(n)} \\
W_0^{(n)} &= a W_T^{(n-1)} + b \int_0^T \gamma^*(t) W_t^{(n-1)} dt \\
&= W_0^{(n-1)} \left(a Y_T^{(n-1)} + b \int_0^T \gamma^*(t) Y_t^{(n-1)} dt\right) \\
&= W_0^{(n-1)} X_n \\
&= W_0 X_1 \cdots X_n
\end{aligned}
$$

where $0 \leq t \leq T$ and $n = 0, 1, 2, \ldots$ with $W_0^{(0)} = W_0$.

We want to determine if it is more likely than not that $W_0^{(n)} > W_0$ for sufficiently large n (that is, is there likely to be growth?).

Multiseason Analysis: Case 1

- Assume $a > 0$ and $b/a \leq 1$ (so, $\gamma^*(t) = 0$)
- In this case, $X_n = a \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right) T + \sigma B_T\right)$
- Thus, $X_n \sim \mathrm{LogN}\left(\left(r - \frac{1}{2}\sigma^2\right) T, \sigma^2 T\right)$

Multiseason Analysis: Case 1

- Hence, the median of X_n is

$$a \cdot \exp\left(\left(r - \frac{1}{2}\sigma^2\right) T\right)$$

- So, for $W_0^{(n)} > W_0$ at least 50% of the time for any n, we need

$$aW_0 \cdot \exp\left(n\left(r - \frac{1}{2}\sigma^2\right) T\right) > W_0$$

$$a > \exp(-rT) \cdot \exp\left(\frac{1}{2}\sigma^2 T\right)$$

Multiseason Analysis: Case 2

- Assume $a = 0$ (annuals) and $r \neq \kappa$ (so, $\gamma^*(t) = \kappa \bar{H}(t - d_A)$)
- In this case,

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

  where $d_A = T - \frac{1}{r-\kappa} \ln\left(\frac{r}{\kappa}\right)$
- We will proceed as in Case 1; however, X_n is not lognormally distributed here, so one has to work "backwards."

Multiseason Analysis: Case 2

One can use the fact that, for sufficiently large n, $X_1 \cdots X_n$ is approximately lognormally distributed (Central Limit Theorem).

Using a formula from Yor, one can then find an upper bound on $\mathrm{Var}(X_n)$ and use this and $E[X_n]$ to find a lower bound for the median of $W_0^{(n)}$ for sufficiently large n.

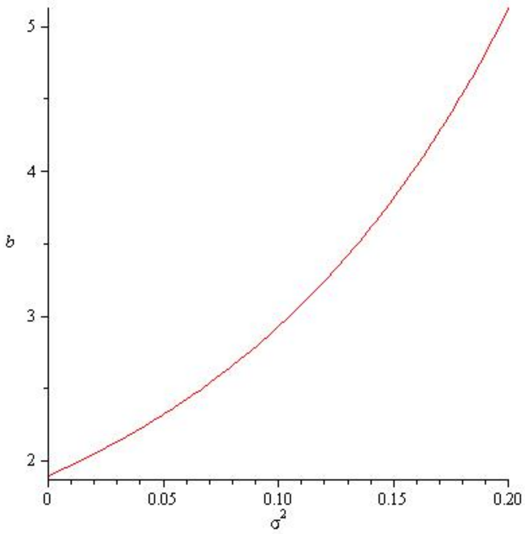
Multiseason Analysis: Case 2

Tying all of these results together, one can show that, to guarantee at least a 50% chance of growth for sufficiently large n, we want

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

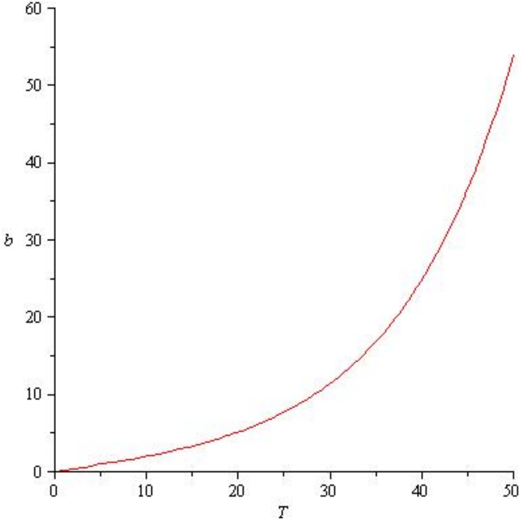
Multiseason Analysis: Case 2 Graphs

$r = 0.0225, k = 0.05, T = 20$



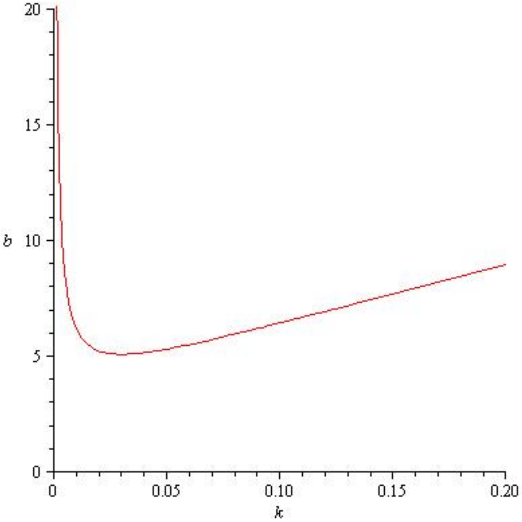
Multiseason Analysis: Case 2 Graphs

$r = 0.0225, k = 0.05, \sigma^2 = 0.2$



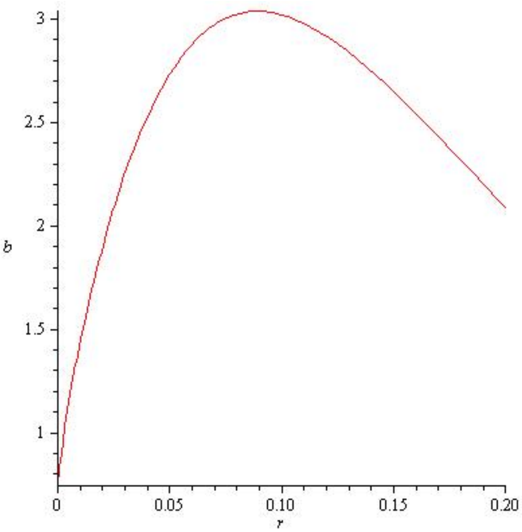
Multiseason Analysis: Case 2 Graphs

$r = 0.03, \sigma^2 = 0.2, T = 20$



Multiseason Analysis: Case 2 Graphs

$k = 0.05, \sigma^2 = 0.2, T = 10$



Comparison of Perennials and Annuals

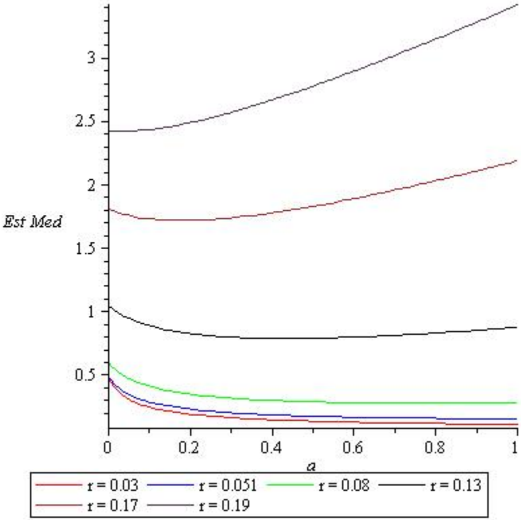
A similar analysis can be done for perennials to arrive at a sufficient condition for at least a 50% chance for growth over a large number of seasons.

Because of the condition's immense messiness (and it looks very similar to the annuals condition), we will not list it here!

It is worth noting, however, that, if we take $a = 0$, then this perennials condition matches the annuals condition.

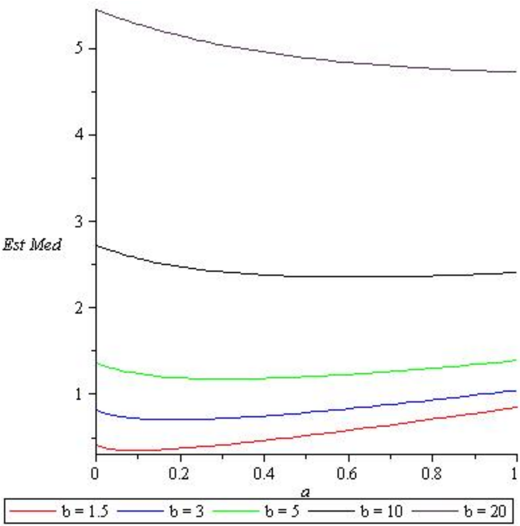
Comparison of Perennials and Annuals Graphs

$b = 5, \kappa = 0.05, \sigma^2 = 0.3, T = 20$



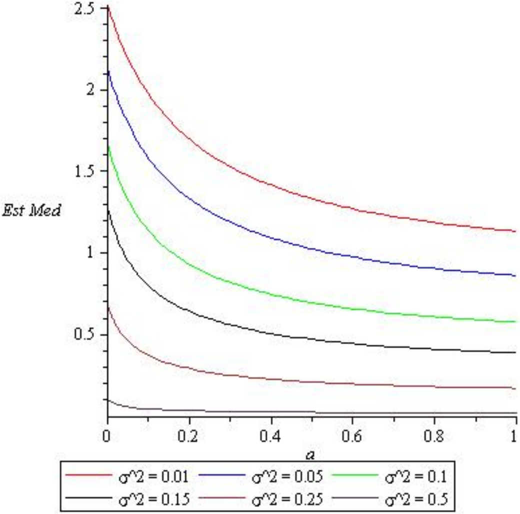
Comparison of Perennials and Annuals Graphs

$r = 0.03, \kappa = 0.05, \sigma^2 = 0.3, T = 20$



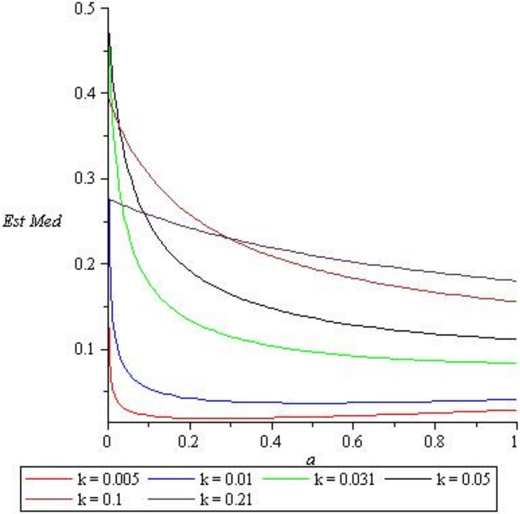
Comparison of Perennials and Annuals Graphs

$b = 5, r = 0.03, \kappa = 0.05, T = 20$



Comparison of Perennials and Annuals Graphs

$b = 5, r = 0.03, \sigma^2 = 0.3, T = 20$



Future Investigations

- Continuing to analyze annuals vs. perennials (multiseason)
- Adding in a drift function to GBM to account for deterministic temperature/rainfall shifts throughout a season (simulation)
- Testing model using estimated parameter values for a specific plant species
- Logistic growth (simulation)
- Other suggestions?

Selected Sources

Yong, Jiongmin et al. *Stochastic Controls*. 1999, Chapters 2, 3, 4, 5, 7.

R. M. Nisbet et al. *From Molecules to Ecosystems through Dynamic Energy Budget Models*. Published in *The Journal of Animal Ecology*, Vol. 69, No. 6 (Nov. 2000), pp. 913-926.

Young, Truman. *A General Model of Comparative Fecundity for Semelparous and Iteroparous Life Histories*. Published in *The American Naturalist*, Vol. 118, No. 1 (July 1981), pp. 27-36.

Yor, Marc. *On Some Exponential Functionals of Brownian Motion*. Published in *Advances in Applied Probability*, Vol. 24, No. 3 (Sep. 1992), pp. 509-531.

Standing at the crossroads
Trying to read the signs
To tell me which way I should go
To find the answer
And all the time I know
Plant your love and let it grow

- Eric Clapton, *Let it Grow* (1974)