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All living organisms must allocate resources to their survival and to their reproduction. In this thesis, we use the mathematics of life history theory to determine the optimal allocation between the two. In particular, we derive equations of optimal allocation using theories of habitat choice and the lifetime fecundity function. We also demonstrate how survival and reproduction can sometimes be measured as positively correlated and yet still represent a trade-off.

SURVIVAL AND REPRODUCTION: OPTIMAL RESOURCE ALLOCATION

by

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# CHAPTER I

## INTRODUCTION

### 1.1 The Problem

Biological organisms are often seen essentially as machines for propagating genetic material [Cha00]. They do this by utilizing obtained resources for reproduction. However, there are many situations that can kill an organism, preventing it from reproducing. Predators, natural disasters, and disease are all dangers that organisms must endure. Thus, organisms must allocate resources not only to their reproduction, but also to their survival.

If an organism allocates too much resource to survival, it will produce fewer offspring than otherwise. Its reproduction will suffer. If, however, an organism allocates too much to reproduction, it will have a greater chance of dying sooner. This will prevent it from participating in future opportunities to reproduce, and its reproduction will again suffer. There must be an optimal ratio of the amount of resource allocated to reproduction versus the amount of resource allocated to survival. For purposes of practicality, resources are measured in units of energy [Bog92], [VNdJ86].

The Principle of Allocation states that if the amount of acquirable resource for two processes that compete directly is constant, then an increase in resources allocated to one process results in a decrease of that of the other process [Ste92].



Survival and reproduction are two necessary functions of life that require energy, so the Principle of Allocation applies to them. But how do living organisms balance these needs?

## 1.2 Context

This is a question of life history theory, the study of patterns of strategies throughout an organism's life. [BHT90] refers to life histories as “lifetime pattern[s] of growth, differentiation, storage and, especially, reproduction.” Studying optimization of life histories provides biologists with a sound foundation to form hypotheses regarding the developments of organisms and populations. These questions result in particular from the subtopic of life history theory known as trade-offs. According to [Ste92], “Trade-offs are the linkages between traits that constrain the simultaneous evolution of two or more traits.” Of these traits, the most commonly studied include current reproduction versus survival, current reproduction versus future reproduction, reproduction versus growth, and number versus quality of offspring [Ste92]. The relationship between the survival and reproduction of a given organism is a well-studied trade-off [Ste92].

## 1.3 Examples

Stearnes [Ste92] provides examples of trade-offs between survival and reproduction. One such example is the beech tree *Fagus sylvatica*, which produce more seeds in ‘mast’ years followed by years of diminished reproduction. Because the diameter of growth rings during mast years is less than that of non-mast years, this is actually an example of growth versus reproduction. However, growth contributes to survivability in many cases.

Stearnes [Ste92] also discusses the mating calls of neotropical frogs. Because certain species of bats locate these frogs and hunt them as prey, the mating calls male frogs emit are necessarily linked to a survival-versus-reproduction trade-off.

## 1.4 Contributions

What amounts of resource should be allocated to survival and to reproduction? What ratio of these traits results in the maximal number of offspring produced over a lifetime? Here, we use the mathematics of life history theory to answer these questions.

In Chapter II, we demonstrate that survival and reproduction do indeed represent a trade-off. Field researchers have shown that allocations to survival and fecundity can sometimes be positively correlated [VNdJ86], but trade-offs are negatively correlated, by definition. We prove, however, that the theory does permit positive correlations when the total amount of resources is not constant. This is done in Theorems 2.1 and 2.2, adapted from [VNdJ86].

In Chapter III, we derive optimal values of amounts of resource allocated to reproduction by maximizing the lifetime fecundity function of organisms. The lifetime fecundity of an organism is the total number of offspring it reproduces over its lifetime. We derive an expression of lifetime fecundity as a function of resources allocated to reproduction in order to find a formula for the resource value that maximizes this function. As adaptations from [Rof84], we find the time at which the maximum of a function related to a fish's fecundity occurs in Lemma 3.1. We also adapt [Rof84] to find the optimal age for a fish to reproduce in Theorems 3.2 and 3.3. Theorem 3.2 represents a semelparously-reproducing species, and Theorem 3.3 represents the iteroparous case. We cover the continuously-reproducing case (Theorem 3.4) and show

that the iteroparous case is better than the continuous case (Theorem 3.5) as original results. Our original results also include an expression of the lifetime fecundity as a function of resources allocated to reproduction (Theorem 3.6) and a derivation of the optimal value allocated to the reproduction in that case (Theorem 3.7).

In Chapter IV, we consider the resource of time rather than conventional energy-based resources. This is done by examining situations in which an organism has a choice between two habitats. Suppose one habitat is associated with a higher mortality rate and a lower growth rate while the other is associated with a lower mortality rate and a higher growth rate. In Theorem 4.1, we prove that the net reproductive rate is maximized when the derivative of the mortality rate by the growth rate is equal to the ratio of the mortality rate to the growth rate, as Gilliam [Gil82] did. Theorem 4.2 is an adaptation of Houston et. al [HMH93], in which we show that the optimal strategy of a fixed-state organism is to minimize its mortality rate-to-growth rate ratio.

CHAPTER II  
POSITIVE AND NEGATIVE CORRELATIONS

de Jong and van Njoordwijk give a model of survival-versus-reproduction trade-offs that explains why positive correlations between these can sometimes be observed [VNdJ86]. Let  $A_i$  be the total amount of resources available to an individual  $i$ ,  $R_i$  be the amount of resources allocated to reproduction, and  $S_i$  be the amount of resources allocated to survival. It is assumed that  $A_i$ ,  $R_i$  and  $S_i$  can be measured in energy units [VNdJ86]. Then, by [VNdJ86],

$$A_i = R_i + S_i \tag{2.1}$$

Additionally, they define a fraction  $B_i$  such that  $B_i = \frac{R_i}{A_i}$  [VNdJ86]. Then, for individual  $i$ ,

$$R_i = B_i A_i \tag{2.2}$$

and

$$S_i = (1 - B_i) A_i \tag{2.3}$$

Suppose  $A_i$  is constant and  $n$  is used a time index. That is, time  $t_0 \equiv 0$  and  $t_{n+1} - t_n = \Delta t$  such that  $t_n = n\Delta t$ . Then, for individual  $i$ ,  $(R_i)_n$  is the amount of resource allocated to reproduction at time  $t_n$  and  $(S_i)_n$  is the amount of resource allocated to survival at time  $t_n$ .

Also,  $\Delta(S_i)_n = (S_i)_{n+1} - (S_i)_n$  and  $\Delta(R_i)_n = (R_i)_{n+1} - (R_i)_n$ . Then, we can represent the set of all possible value pairs of  $R_i$  and  $S_i$  by the portion of the line  $S_i = -R_i + A_i$  that is in the first quadrant of the  $S_i$  versus  $R_i$  plane. Every point  $p_i$  on this line is given by  $p_i = (R_i, S_i)$ , describing the balance between the energy allocated to reproduction and the energy allocated to survival.

Table 1. Notation

Symbol	Description
$A_i$	Total amount of resource available to individual $i$
$R_i$	Amount of resources allocated to reproduction by individual $i$
$S_i$	Amount of resources allocated to survival by individual $i$
$B_i$	Fraction $\frac{R_i}{A_i}$ for individual $i$
$(R_i)_n$	Amount of resource allocated to reproduction by individual $i$ at time $t_n$
$(S_i)_n$	Amount of resource allocated to survival by individual $i$ at time $t_n$
$\Delta(S_i)_n$	Given time $t_n$ , $\Delta(S_i)_n = (S_i)_{n+1} - (S_i)_n$
$\Delta(R_i)_n$	Given time $t_n$ , $\Delta(R_i)_n = (R_i)_{n+1} - (R_i)_n$
$p_i(t_n)$	$((R_i)_n, (S_i)_n)$
$A_{min}$	Minimum total resource available
$A_{max}$	Maximum total resource available
$\text{range}(A_i)$	$[A_{min}, A_{max}]$

For a given individual  $i$  with constant total resource  $A_i$ , there exists a point  $p_i$  that scales along the line  $S_i = -R_i + A_i$  when the individual increases or decreases the energy allocated to one of the two traits. Thus, we can define the function  $p_i(t_n)$  that gives the location of the point  $p_i$  at time  $t_n$ , so that  $p_i(t_n) = ((R_i)_n, (S_i)_n)$ .

It is simple to show that any change in one trait results in an equal but opposite change in the other:

**Theorem 2.1** (Adapted from [VNdJ86]). *For individual  $i$  with constant total resource  $A_i$ ,  $\Delta(R_i)_n = -\Delta(S_i)_n$ .*

*Proof.*

$$A_i = (S_i)_{n+1} + (R_i)_{n+1} = (S_i)_n + (R_i)_n \quad (2.4)$$

$$(R_i)_{n+1} - (R_i)_n = (S_i)_n - (S_i)_{n+1} \quad (2.5)$$

Therefore,

$$\Delta(R_i)_n = -\Delta(S_i)_n. \quad (2.6)$$

□

This phenomenon of equal-but-opposite change is an example of negative correlation in the two traits. Thus, when  $A_i$  is held constant, the amount of resource allocated to survival and the amount of resource allocated to reproduction are negatively correlated. This is demonstrated in Figure 1. However, this is not necessarily the case when  $A_i$  is not held constant. For a given individual  $i$ ,  $\text{range}(A_i) \equiv [A_{min}, A_{max}]$ , where  $A_{min}$  is the minimum possible total resource the individual can have and still live and  $A_{max}$  is the maximum total resource the individual can have.

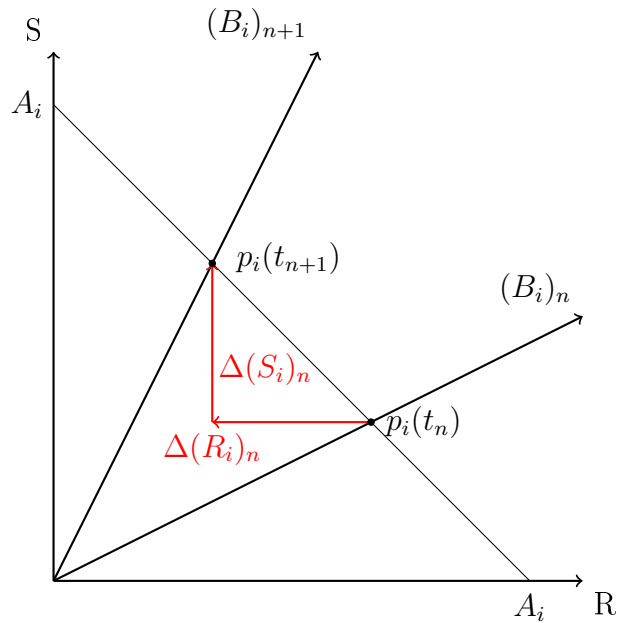


Figure 1. When  $A_i$  is held constant and  $B_i$  varies from  $p_i(t_n)$  to  $p_i(t_{n+1})$ ,  $\Delta(S_i)_n = -\Delta(R_i)_n$ . Note that  $\Delta(S_i)_n$  is positive and  $\Delta(R_i)_n$  is negative.

When  $\text{range}(A_i)$  has a width greater than zero, vertical and horizontal motion of  $p_i$  is possible. This sort of motion implies neutral correlation because the value of one trait can change without the value of the other doing the same. This neutral correlation is demonstrated in Figure 2. However, motion along the boundaries ( $A_i = A_{min}$  or  $A_{max}$ ) results again in equal-but-opposite negative correlation between reproduction and survival. Of course, this sort of motion is simply a result of the case of constant  $A_i$ .

**Theorem 2.2** (Adapted from [VNdJ86]). *If  $\text{range}(A_i) > 0$  and  $B_i$  is held constant, then there exists a positive correlation between  $R_i$  and  $S_i$ .*

*Proof.* Suppose  $B_i$  is held constant. Then,  $\frac{R_i}{A_i}$  is constant.

$$\frac{(R_i)_n}{(A_i)_n} = \frac{(R_i)_{n+1}}{(A_i)_{n+1}} \quad (2.7)$$

$$(R_i)_n(A_i)_{n+1} = (R_i)_{n+1}(A_i)_n \quad (2.8)$$

$$(R_i)_n[(R_i)_{n+1} + (S_i)_{n+1}] = (R_i)_{n+1}[(R_i)_n + (S_i)_n] \quad (2.9)$$

$$(R_i)_n(R_i)_{n+1} + (R_i)_n(S_i)_{n+1} = (R_i)_{n+1}(R_i)_n + (R_i)_{n+1}(S_i)_n \quad (2.10)$$

$$(R_i)_n(S_i)_{n+1} = (R_i)_{n+1}(S_i)_n \quad (2.11)$$

$$\frac{(R_i)_n}{(R_i)_{n+1}} = \frac{(S_i)_n}{(S_i)_{n+1}} \quad (2.12)$$

Note that all values of  $R_i$  and  $S_i$  are positive.

This implies that if  $(R_i)_{n+1} > (R_i)_n$ , then  $(S_i)_{n+1} > (S_i)_n$ . Similarly,  $(R_i)_{n+1} < (R_i)_n$  implies that  $(S_i)_{n+1} < (S_i)_n$ , and  $(R_i)_{n+1} = (R_i)_n$  implies that  $(S_i)_{n+1} = (S_i)_n$ .

Therefore, there exists a positive correlation between  $R_i$  and  $S_i$ . □



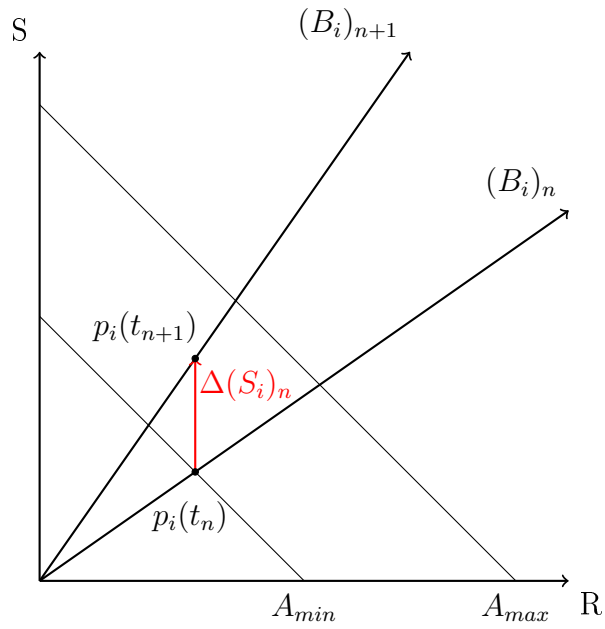


Figure 2. When neither  $A_i$  nor  $B_i$  is held constant, the correlation between  $S_i$  and  $R_i$  can be neutral. Note that, in this figure,  $\Delta(S_i)_n$  is positive and  $\Delta(R_i)_n = 0$ .

Theorems 2.1 and 2.2 describe the cases of positive and negative correlation between survival and reproduction. When the total amount of resource is held constant, these traits have a negative correlation; when the ratio between these traits is held constant, they have a positive correlation.

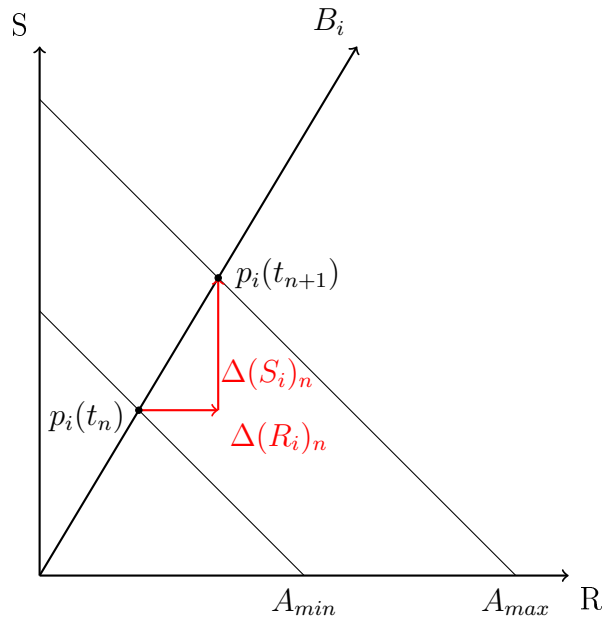


Figure 3. When  $B$  is held constant and  $A$  varies, the sign of  $\Delta S$  is the sign of  $\Delta R$ . Note that in this figure, both  $\Delta S$  and  $\Delta R$  are positive.

This is why van Noordwijk and de Jong [VNdJ86] claim that positive correlations are seen in individuals  $i$  such that  $\text{range}(A_i)$  is large and variation in  $B_i$  is small and that negative correlations are seen in individuals such that  $\text{range}(A_i)$  is small and variation in  $B_i$  is large. The case of a positive correlation is illustrated in Figure 3.

CHAPTER III  
FECUNDITY

**3.1 Introduction**

One of the most important concepts in ecology is fecundity. The *fecundity* of an individual is the number of offspring that it produces [BHT90]. Fecundity has such a clear association to fitness that understanding the nature of the fecundity of an organism improves understanding of that organism's ecological behaviors.

Table 2. Notation

Symbol	Description
$f(t)$	Fecundity function
$\ell(t)$	Probability of survival to age $t$
$m(t)$	Number of female offspring a female of age $t$ can produce at time $t$
$T$	Earliest age of reproduction
$F(T)$	Lifetime fecundity
$a$	Fecundity coefficient
$L_\infty$	Asymptotic length of a fish species
$p$	Probability of surviving the larval stage
$M$	Instantaneous mortality rate
$C$	Constant of the form $paL_\infty^3$

Because of this connection, life history theorists use the *fecundity function*  $f(t)$ , (3.1), as a model for understanding optimal strategies for reproduction.

The expected number of female offspring a female of age  $t$  can produce at that age is  $f(t)$ . Because a female can die before reaching age  $t$ ,

$$f(t) = \ell(t)m(t), \tag{3.1}$$

where  $\ell(t)$  represents the probability of a female surviving to age  $t$  and  $m(t)$  is the number of female offspring that a female of age  $t$  can produce. In this manner, the fecundity function conveys the importance of reproductive investments. Low values of  $f(t)$  can correspond to low survival probabilities  $\ell(t)$ , low values of  $m(t)$ , or both.

Table 3. Life History Terminology

<b>Term</b>	<b>Definition</b>
fecundity	The <i>fecundity</i> of an individual is the number of offspring it produces.
fecundity function	The <i>fecundity function</i> gives the expected number of female offspring a female of age $t$ can produce.
lifetime fecundity	The <i>lifetime fecundity</i> of an organism is the expected total number of female offspring a female can produce over her lifetime.
asymptotic length	The <i>asymptotic length</i> of a species is a length to which the average member of that species grows asymptotically with time.
instantaneous rate of mortality	The <i>instantaneous rate of mortality</i> is the instantaneous rate at which individuals die.
iteroparous	An <i>iteroparous species</i> is a species that reproduces seasonally (i.e. once every year).
semelparous	A <i>semelparous species</i> is a species that reproduces once in its lifetime.
determinate growth	An organism is said to have <i>determinate growth</i> if growth ceases after the earliest age of reproduction
indeterminate growth	An organism is said to have <i>indeterminate growth</i> if growth continues after reproduction.

Another benefit of the fecundity function is its use in determining when an organism should save its energy for later reproduction. For example, the fecundity of an organism can be altered by changing its earliest age of reproduction. It is clear that the total number of offspring of two individuals with equal life spans and reproductive rates will only differ if their respective first ages of reproduction are not the same. Roff [Rof84] refers to this variable as the age of maturity  $T$ .

Ultimately, what we wish to know about an organism's success can often be summarized as the total number of offspring produced. All things being equal, the probability of offspring surviving to reproduce is higher for an individual that produces more offspring than another. The *lifetime fecundity function*  $F(T)$  is the average total number of female offspring a female can produce across her lifetime, given she began reproduction at age  $T$ . We have

$$F(T) = \sum_{t=T}^{\infty} f(t). \quad (3.2)$$

### 3.2 Roff's Fecundity Model

Roff [Rof84] developed formulas for  $f(t)$  and  $m(t)$  to describe the ecological and life history properties of fish species often found in fisheries. Experimental evidence indicates that the number of offspring many commercial fish produce is a function of the length. In fact, measurements have indicated that the fecundity of fish is proportional to a power of length very close to 3. Thus,

$$m(t) = aL^3(t), \quad (3.3)$$

where  $a$  is a constant. Fish of many species grow to a maximum length asymptotically. Using the notation  $L_\infty$  for asymptotic length, Roff uses the growth equation

$$L(t) = L_\infty(1 - e^{-kt}), \quad (3.4)$$

where  $k$  is a growth constant. It is important to note here that (3.4) describes *indeterminate growth*; that is, growth does not cease at the first age of reproduction. *Determinate growth* would incorporate a constant length after the first age of reproduction. Thus, indeterminate growth of females implies that  $m(t)$  is

$$m(t) = aL_\infty^3(1 - e^{-kt})^3. \quad (3.5)$$

Next, Roff [Rof84] derives an expression for  $\ell(t)$ :

$$\ell(t) = pe^{-Mt}. \quad (3.6)$$

Here,  $p$  represents the probability of surviving the larval stage of a fish, and  $M$  is the *instantaneous rate of mortality*.  $M$  serves as a measure of danger in the fish's environment by describing the average rate at which fish of the given species die in the given environment.

Consequently, the fecundity of a fish of indeterminate growth can be described as

$$f(t) = pe^{-Mt}aL_\infty^3(1 - e^{-kt})^3. \quad (3.7)$$

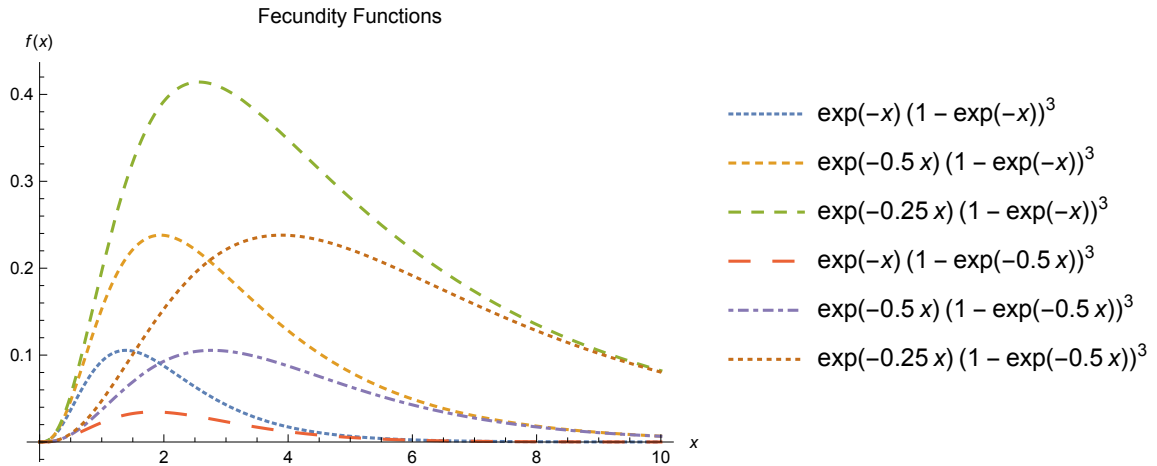


Figure 4. This is a collection of graphs of the form  $y = e^{-Mx}(1 - e^{-kx})^3$ . Values for  $M$  are given as 0.25, 0.5, and 1. Values for  $k$  are given as 0.5 and 1.

See Figure 4 for illustration.  $f(t)$  is also useful for understanding the fecundity of determinate fish. This is because the fecundity function of a fish of determinate growth is identical to that of indeterminate growth until the age  $T$  of first reproduction.

In order to incorporate a cost to reproduction, Roff [Rof84] assumes that growth is *determinate*; that is, its growth ceases at the first age of reproduction. Also, Roff considers two forms of reproduction: *semelparous* and *iteroparous*. A species is iteroparous if it breeds seasonally, and it is semelparous if it only breeds once in its lifetime.

Examples include the sand goby (*Pomatoschistus minutus*), which is an iteroparous breeder, and the sea lamprey (*Petromyzon marinus*), which reproduces semelparously [LMJ+16]. Under the assumption of determinate growth,

$$m(t) = \begin{cases} aL_\infty^3(1 - e^{-kt}) & \text{if } t < T, \\ aL_\infty^3(1 - e^{-kT}) & \text{if } t \geq T, \end{cases} \quad (3.8)$$

$$f(t) = \begin{cases} Ce^{-Mt}(1 - e^{-kt})^3 & \text{if } t < T, \\ Ce^{-Mt}(1 - e^{-kT})^3 & \text{if } t \geq T, \end{cases} \quad (3.9)$$

where  $C = paL_\infty^3$ . And so, by (3.2),

$$F(T) = \sum_{t=T}^{\infty} Ce^{-Mt}(1 - e^{-kT})^3. \quad (3.10)$$

An example of  $f(t)$  is given in Figure 5.

### 3.3 Roff's Fecundity Theorems

**Lemma 3.1** (Adapted from [Rof84]). *The maximum of the function  $g(t) = Ce^{-Mt}(1 - e^{-kt})^3$  occurs at age  $t = \frac{1}{k} \ln\left(\frac{M+3k}{M}\right)$ .*

*Proof.*

$$\frac{dg}{dt} = -CMe^{-Mt}(1 - e^{-kt})^3 + 3kCe^{-kt}e^{-Mt}(1 - e^{-kt})^2. \quad (3.11)$$



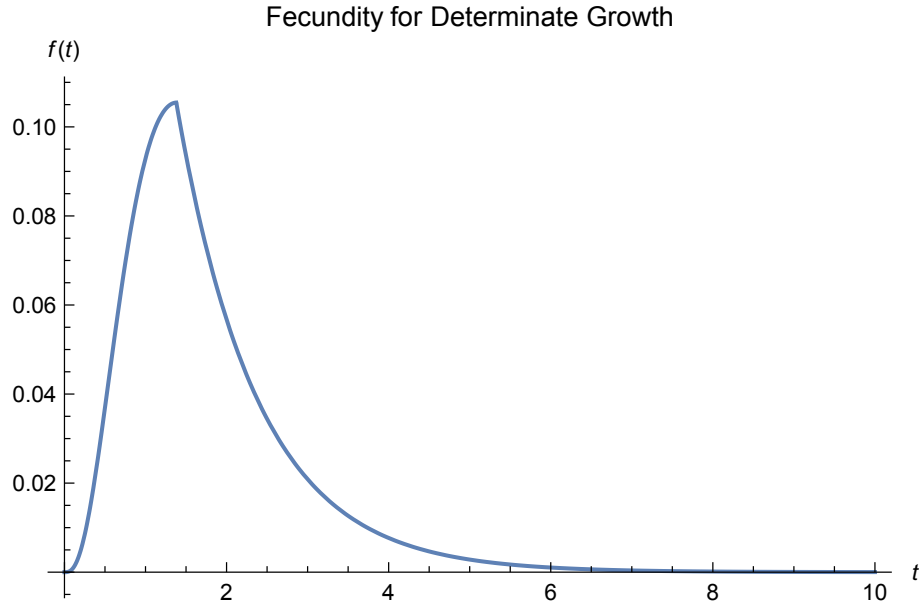


Figure 5. A graph of the fecundity function  $f(t)$  for a fish of determinate growth whose earliest age of reproduction,  $t = 1.38$ , is approximately the optimal age for first reproduction. Observe that  $f(t) = e^{-t}(1 - e^{-t})^3$  when  $t < 1.38$ , and  $f(t) = e^{-t}(1 - e^{-1.38})^3$  when  $t \geq 1.38$ .

Let  $\frac{dq}{dt} = 0$ . Then, solving for  $t$ , we obtain

$$M(1 - e^{-kt}) = 3ke^{-kt} \quad (3.12)$$

$$M = (M + 3k)e^{-kt} \quad (3.13)$$

$$t = \frac{1}{k} \ln \left( \frac{M + 3k}{M} \right) \quad (3.14)$$

$$> 0. \quad (3.15)$$

Note that  $\frac{dg}{dt}$  is negative when  $CMe^{-Mt}(1 - e^{-kt})^3 > 3kCe^{-kt}e^{-Mt}(1 - e^{-kt})^2$ , and  $\frac{dg}{dt}$  is positive when  $CMe^{-Mt}(1 - e^{-kt})^3 < 3kCe^{-kt}e^{-Mt}(1 - e^{-kt})^2$ . Therefore, the maximum of  $g(t)$  indeed occurs for  $t$  given in (3.14).  $\square$

**Theorem 3.2** (Adapted from [Rof84]). *In the case of a semelparous fish species of determinate growth, the optimal value of  $T$  is given by  $T = \frac{1}{k} \ln \left( \frac{M+3k}{M} \right)$ .*

*Proof.* Since the species only reproduces once, we have, by (3.9),  $F(T) = f(T) = Ce^{-MT}(1 - e^{-kT})^3$ . Therefore, the result follows from Lemma 3.1.  $\square$

**Theorem 3.3** (Adapted from [Rof84]). *In the case of an iteroparous fish species of determinate growth, the optimal value of  $T$  is given by  $T = \frac{1}{k} \ln \left( \frac{M+3k}{M} \right)$ .*

*Proof.*

$$F(T) = \sum_{t=T}^{\infty} Ce^{-Mt}(1 - e^{-kt})^3 \quad (3.16)$$

$$= C(1 - e^{-kT})^3 \left( \sum_{t=T}^{\infty} e^{-Mt} \right) \quad (3.17)$$

$$= C(1 - e^{-kT})^3 \left( \frac{e^{-MT}}{1 - e^{-M}} \right) \quad (3.18)$$

$$= \frac{Ce^{-MT}(1 - e^{-kT})^3}{1 - e^{-M}} \quad (3.19)$$

$$= \frac{g(T)}{1 - e^{-M}}. \quad (3.20)$$

Note that  $\frac{1}{1-e^{-M}}$  is a constant. Then, by Lemma 3.1, the value of  $T$  maximizing  $F(T)$  is given by  $T = \frac{1}{k} \ln \left( \frac{M+3k}{M} \right)$ .  $\square$

**Theorem 3.4.** *In the case of a continuously-reproducing fish species of determinate growth, the optimal value of  $T$  is given by  $T = \frac{1}{k} \ln \left( \frac{M+3k}{M} \right)$ .*

*Proof.*

$$F(T) = \int_T^\infty C e^{-Mt} (1 - e^{-kT})^3 dt \quad (3.21)$$

$$= \frac{C e^{-Mt} (1 - e^{-kT})^3}{(-M)} \Big|_T^\infty$$

$$= \lim_{x \rightarrow \infty} \left[ \frac{C e^{-Mx} (1 - e^{-kT})^3}{(-M)} - \frac{C e^{-MT} (1 - e^{-kT})^3}{(-M)} \right]$$

$$= \frac{C e^{-MT} (1 - e^{-kT})^3}{M}$$

$$= \frac{g(T)}{M}. \quad (3.22)$$

Therefore, by Lemma 3.1, the value of  $T$  maximizing  $F(T)$  is given by  $T = \frac{1}{k} \ln \left( \frac{M+3k}{M} \right)$ .  $\square$

**Theorem 3.5.**  $F_{iteroparous}(T) \geq F_{continuous}(T)$  given that all other species characteristics are equal.

*Proof.* By (3.20),

$$F_{iteroparous}(T) = \frac{g(T)}{1 - e^{-M}}. \quad (3.23)$$

By (3.22),

$$F_{continuous}(T) = \frac{g(T)}{M}. \quad (3.24)$$

Note that

$$1 - M \leq e^{-M} \quad (3.25)$$

and, therefore, the result follows.  $\square$

### 3.4 Connections to Allocation

Many interesting results follow from Roff's fecundity model presented in Section 3.2, but the model so far made no connection between fecundity and resource allocation. In this section, we will develop this connection, and we will then use the optimization of fecundity to determine optimal patterns of allocation.

Let  $A(t)$  be the function describing the amount of resource an individual has at time  $t$ ,  $R(t)$  be the amount allocated to reproduction, and  $S(t)$  be the amount allocated to survival. As in Chapter II, we have

$$A(t) = R(t) + S(t). \quad (3.26)$$

Let  $m(t)$  be the number of female offspring a female at age  $t$  can produce at age  $t$ . Because each offspring can be represented as the amount of resource required to produce it, we assume  $m(t)$  is proportional to the amount of energy allocated to reproduction. That is, for some constant  $q$ ,

$$m(t) = qR(t). \quad (3.27)$$

We also develop a model describing how values of  $S(t)$  impact fecundity. Fischer, Taborsky, and Dieckmann [FTD09] developed a model simulating an individual allocating energy to multiple biological traits in stochastic environments.

This model is iterative, with distinct times. They describe the probability  $b$  that an individual survives from time  $\tau$  to  $\tau + 1$  as the ratio of energy allocated to survival at that time to the sum of that energy and a constant  $S_{1/2}$  of the environment.  $S_{1/2}$  is the value for resource allocation at which probability  $b$  becomes 1/2. The probability of surviving from time  $\tau$  to time  $\tau + 1$  is thus

$$b(\tau) = \frac{S(\tau)}{S(\tau) + S_{1/2}} \quad (3.28)$$

for  $\tau = 0, 1, 2, 3, \dots$ . The function  $\ell(t)$  represents the probability of surviving from age 0 to age  $t$ , so

$$\ell(t) = \prod_{\tau=0}^{t-1} b(\tau) \quad (3.29)$$

$$= \prod_{\tau=0}^{t-1} \frac{S(\tau)}{S(\tau) + S_{1/2}} \quad (3.30)$$

Table 4. Notation

<b>Symbol</b>	<b>Description</b>
$A(t)$	Total energy available at time $t$
$R(t)$	Amount of energy allocated to reproduction at time $t$
$S(t)$	Amount of energy allocated to survival at time $t$
$f(t)$	Fecundity function
$m(t)$	Number of female offspring a female of age $t$ can produce at time $t$
$\ell(t)$	Probability of survival to age $t$ from age 0
$q$	Constant such that $m(t) = qR(t)$
$b(\tau)$	Probability of surviving from time $\tau$ to $\tau + 1$
$S_{1/2}$	Energy allocation necessary for probability of survival from $t$ to $t + 1$ to be 1/2
$T$	Earliest age of reproduction
$v$	Probability of surviving to the age of first reproduction $T$

As a result,

$$\begin{aligned} f(t) &= \ell(t)m(t) \\ &= qR(t) \prod_{\tau=0}^{t-1} \frac{S(\tau)}{S(\tau) + S_{1/2}} \end{aligned} \tag{3.31}$$

Note, however, that the probability of surviving to age  $T$  is given by

$$\ell(T) = \prod_{\tau=0}^{T-1} \frac{A(\tau)}{A(\tau) + S_{1/2}} \tag{3.32}$$

For simplicity, we will denote the probability of surviving to age  $T$  as  $v$ . Thus, for all times  $t > T$ , the fecundity function is given as

$$f(t) = qvR(t) \prod_{\tau=T}^{t-1} \frac{S(\tau)}{S(\tau) + S_{1/2}} \tag{3.33}$$

This describes an organism's fecundity in terms of the resources it has allocated to survival and to reproduction.

Recall that an organism's reproductive success is maximized with its lifetime fecundity  $F(T)$ , which is determined by fecundity  $f(t)$ . The optimal balance between  $R(t)$  and  $S(t)$  is that which maximizes the lifetime fecundity  $F(T)$ , which is found as

$$F(T) = \sum_{t=T}^{\infty} f(t) \quad (3.34)$$

$$= qv \sum_{t=T}^{\infty} \left( R(t) \prod_{\tau=T}^{t-1} \frac{S(\tau)}{S(\tau) + S_{1/2}} \right). \quad (3.35)$$

**Theorem 3.6.** *When  $A(t) = A$ ,  $S(t) = S$ ,  $R(t) = R$  for all  $t > T$ ,  $F(T) = qvR \left( \frac{S+S_{1/2}}{S_{1/2}} \right)$ .*

*Proof.* Note that

$$F(T) = qvR \sum_{t=T}^{\infty} \left( \prod_{\tau=T}^{t-1} \frac{S}{S + S_{1/2}} \right) \quad (3.36)$$

$$= qvR \sum_{t=T}^{\infty} \left( \frac{S}{S + S_{1/2}} \right)^{t-T} \quad (3.37)$$

$$= qvR \sum_{t=0}^{\infty} \left( \frac{S}{S + S_{1/2}} \right)^t \quad (3.38)$$

$$= qvR \left( \frac{S + S_{1/2}}{S_{1/2}} \right), \quad (3.39)$$

because the series of (3.38) is geometric. □



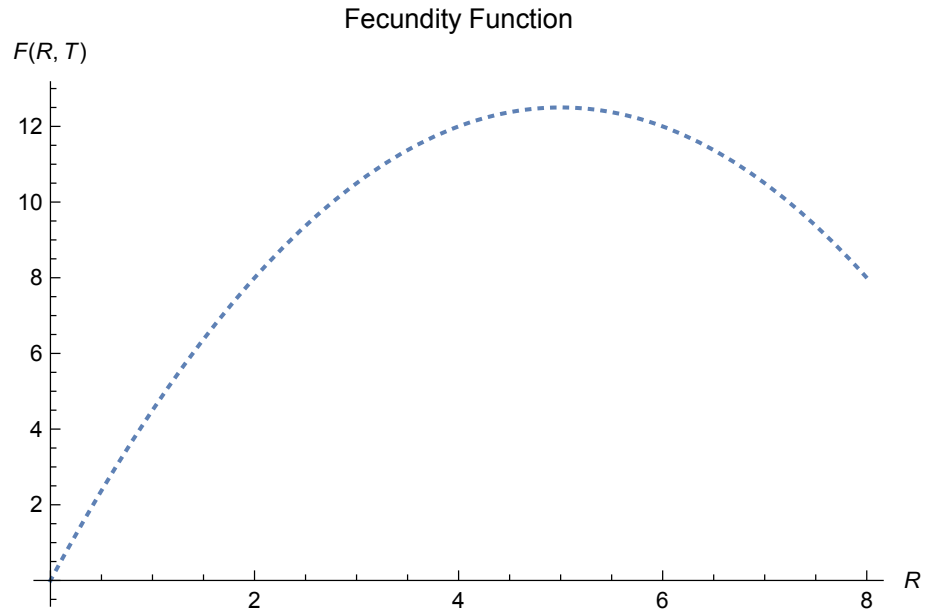


Figure 6. This is a graph of  $F$  with respect to  $R$ . Here, we set  $q = 1$ ,  $v = 1$ ,  $A = 8$ , and  $S_{1/2} = 2$ .

Note that  $F$  can be rewritten in terms of  $R$ :

$$F(R, T) = \frac{qvR(A - R + S_{1/2})}{S_{1/2}}. \quad (3.40)$$

$F$  is illustrated as a function of  $R$  for multiple values of  $T$  in Figure 6.

**Theorem 3.7.** *When  $A(t) = A$ ,  $S(t) = S$ , and  $R(t) = R$  for all  $t > T$  and  $S_{1/2} < A$ , the value of  $R$  that maximizes  $F(R, T)$  is given by  $R = \frac{A+S_{1/2}}{2}$ .*

*Proof.*

$$\frac{\partial F}{\partial R} = \frac{qv(A - R + S_{1/2}) - qvR}{S_{1/2}} \quad (3.41)$$

$$= \frac{qv(A + S_{1/2} - 2R)}{S_{1/2}} \quad (3.42)$$

Letting  $\frac{\partial F}{\partial R} = 0$ , we obtain the optimal value for  $R$ :

$$R = \frac{A + S_{1/2}}{2} \quad (3.43)$$

This represents the optimal value of  $R$ , because  $F$  is clearly a concave function of  $R$ . □

$A$  and  $S_{1/2}$  are the only two terms included in (3.43). With only some simple notation and some basic knowledge of resource allocation's connections to the lifetime fecundity of an organism, a description of an optimal value for  $R$  can be found.

CHAPTER IV  
RISK AND REWARD

**4.1 Gilliam Outline**

In his Ph.D. thesis, Gilliam [Gil82] considers fish species that have the option of spending varying amounts of time in two different habitats. One habitat has a low availability of food, but it also has a low predator density; in the other habitat, the rates of both food consumption and predation are higher. By constructing an appropriate optimal control problem and building the associated Hamiltonian of optimal control theory, Gilliam was able to derive a strategy for fish in these situations based on their growth rates.

Table 5. Notation

<b>Symbol</b>	<b>Definition</b>
$R_0$	Net reproductive rate
$\ell(t)$	Probability of survival to age $t$
$m(t)$	Reproductive rate at age $t$
$\mu(t)$	Mortality rate (probability of death per unit time)
$D(t)$	Probability of death by age $t$
$T$	Final age
$s(t)$	Size at age $t$
$H(t)$	Hamiltonian function
$g(t)$	Growth rate at age $t$
$\lambda_x$	Costate variable of state $x$

Gilliam [Gil82] uses the function  $\mu(t)$  to describe the mortality rate at time  $t$ . The mortality rate of an individual is its probability of death per unit time. In Gilliam's model, the mortality rate of a fish at a given time will be determined by the habitat it currently occupies. Gilliam uses the function  $D(t)$  to describe a fish's probability of dying by age  $t$ . Thus,

$$D(t) = \int_0^t \mu(\tau) d\tau, \quad (4.1)$$

where  $\tau$  is a dummy variable for age. Note that the probability of survival from age  $t$  to age  $t + dt$  is given by  $1 - \mu(t)dt \approx e^{-\mu(t)dt}$ . For a discrete-time model,  $\ell(t) \approx \prod_{\tau=0}^t e^{-\mu(\tau)d\tau} = e^{-\sum_{\tau=0}^t \mu(\tau)d\tau}$ . Thus, for a continuous model like Gilliam's,

$$\ell(t) = e^{-\int_{\tau=0}^t \mu(\tau) d\tau} = e^{-D(t)}. \quad (4.2)$$

A fish's strategy will be optimal when its net reproductive rate is maximal. The net reproductive rate is given as

$$R_0 = \int_0^{\infty} \ell(t)m(t)dt \quad (4.3)$$

$$= \int_0^{\infty} e^{-D(t)}m(t)dt \quad (4.4)$$

$$= \lim_{T \rightarrow \infty} \int_0^T e^{-D(t)}m(t)dt. \quad (4.5)$$

In order to find the maximum value of  $R_0$ , Gilliam constructs an optimal control problem and the associated Hamiltonian. In general, for an equation

$$J = \int_0^T L(x(t), u(t)) dt, \quad (4.6)$$

with states  $x(t)$  and control  $u(t)$ , the control Hamiltonian takes the form

$$H(x, u, \lambda, t) = L(x(t), u(t)) + \lambda(t) \frac{dx}{dt}, \quad (4.7)$$

where  $\lambda(t)$  is the costate variable of  $x$ . Pontryagin's Maximum Principle [Ber13], [SW97] states that  $J$  is maximized when the following four conditions are met:

$$\frac{d\lambda}{dt} = -\frac{\partial H}{\partial x}, \quad (4.8)$$

$$\frac{dx}{dt} = \frac{\partial H}{\partial \lambda}, \quad (4.9)$$

$$\frac{\partial H}{\partial u} = 0, \quad (4.10)$$

and there exists a constant  $\lambda_0$  such that

$$(\lambda(t), \lambda_0) \neq (0, 0) \quad (4.11)$$

for all times  $t$ . Additionally,  $\frac{\partial H}{\partial t} = 0$  if  $H$  is not explicitly dependent upon  $t$ .

**Theorem 4.1** (Adapted from [Gil82]).  $R_0$  is maximized when  $\frac{\partial \mu}{\partial g} = \frac{\mu}{g}$ .

*Proof.* The corresponding control Hamiltonian of  $R_0 = \int_0^\infty e^{-D(t)} m(t) dt$  is given by

$$H(D, s, \lambda_D, \lambda_s, g, t) = L(D(t), s(t), g(t)) + \lambda_D(t) \frac{dD}{dt} + \lambda_s(t) \frac{ds}{dt} \quad (4.12)$$

$$= e^{-D(t)} m(s(t)) + \lambda_D(t) \mu(g(t), s(t)) + \lambda_s(t) g(t). \quad (4.13)$$

Here,  $R_0$  is the variable we wish to maximize. The states of  $R_0$  are  $D(t)$  and  $s(t)$ , where  $s(t)$  is the size of the individual at time  $t$ . Similarly,  $L = e^{-D(t)} m(s(t))$ , and the costate variables are the  $\lambda$ -variables corresponding to  $D$  and  $s$ . The control of  $R_0$  is the growth function

$$g(t) = \frac{ds}{dt}. \quad (4.14)$$

By Pontryagin's Maximum Principle,  $R_0$  is maximized only when

$$\frac{\partial H}{\partial g} = 0. \quad (4.15)$$

Then, because  $\frac{\partial H}{\partial g} = \lambda_D(t) \frac{\partial \mu}{\partial g} + \lambda_s$ ,

$$\frac{\partial \mu}{\partial g} = -\frac{\lambda_s}{\lambda_D} \quad (4.16)$$

when  $R_0$  is maximized.

Note that

$$\lim_{T \rightarrow \infty} e^{-D(T)}m(T) = \lim_{T \rightarrow \infty} \ell(T)m(T) = 0 \quad (4.17)$$

because the individual would otherwise live indefinitely. Additionally, by [Gil82],

$$\lim_{T \rightarrow \infty} \lambda_D(T) = \lim_{T \rightarrow \infty} \lambda_s(T) = 0. \quad (4.18)$$

Then,

$$\lim_{T \rightarrow \infty} H(T) = 0. \quad (4.19)$$

Note that  $H$  is not explicitly dependent upon  $t$ , and thus,

$$H = 0 \quad (4.20)$$

for all values of  $t$ . Then,

$$e^{-D}m + \lambda_D\mu + \lambda_s g = 0. \quad (4.21)$$

Solving for  $\lambda_s$ , we find

$$\lambda_s = -\frac{e^{-D}m + \lambda_D\mu}{g}. \quad (4.22)$$

Then, by (4.16),

$$\frac{\partial \mu}{\partial g} = \frac{\left( \frac{e^{-D(t)} m(t)}{\lambda_D(t)} \right) + \mu(t)}{g(t)} \quad (4.23)$$

for all times  $t$ . At all times  $t$  such that the individual in question is juvenile,  $m(t) = 0$ . As a result, (4.23) reduces to

$$\frac{\partial \mu}{\partial g} = \frac{\mu}{g}. \quad (4.24)$$

□

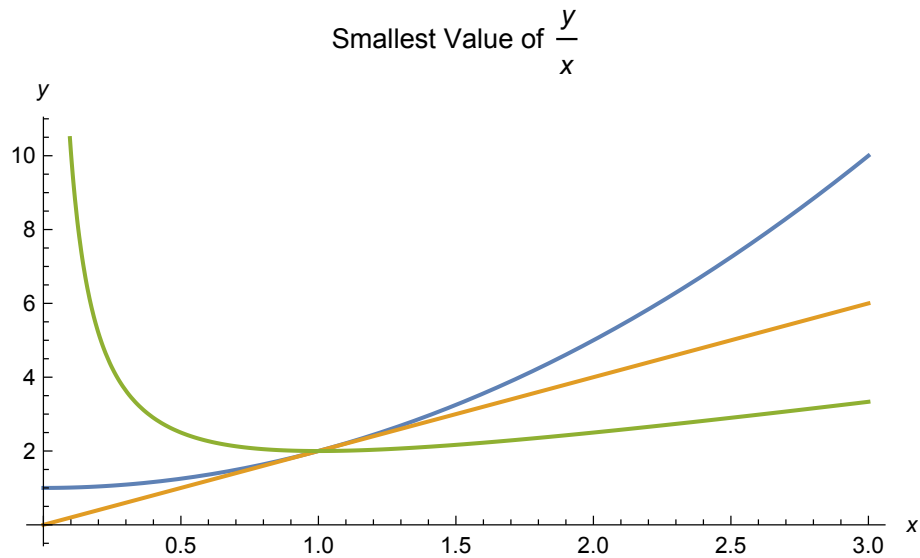


Figure 7. If  $y$  is a strictly increasing curve of  $x$ , the minimal value of  $\frac{y}{x}$  is the one that acts as the slope of the line that is tangent to  $y$ . Here,  $y = x^2 + 1$  and the minimal value of  $\frac{y}{x}$  is 2. The green curve represents  $\frac{y}{x}$  as a function.



Because the rate of predation increases with food availability,  $\mu$  is an increasing function of  $g$ . As in Chapter II, we can graphically represent a fraction as a line passing through the origin; the slope of that line is equal to the fraction in question. Thus, values of  $\frac{\mu}{g}$  can be represented as lines on a  $\mu$ -vs- $g$  plot. We find that, because  $\mu$  is strictly increasing in  $g$ , the smallest value of  $\frac{\mu}{g}$  is represented by a line tangent to the curve  $\mu$ . Figure 7 demonstrates this phenomenon graphically. As a result,  $\frac{\partial \mu}{\partial g} = \frac{\mu}{g}$  only when  $\frac{\mu}{g}$  is minimized. The *Gilliam Rule* thus states to minimize  $\frac{\mu}{g}$  in order to maximize  $R_0$ .

## 4.2 Houston, McNamara, Hutchinson Model

Houston, McNamara, and Hutchinson [HMH93] look at trade-offs between energy gain and risk of predation. In many cases, survival of an individual is likelier in low-energy environments and reproduction is likelier with greater acquisition of resources [HMH93]. Houston et. al describe this model as one in which “High rates of gain can be achieved only at the cost of a high rate of predation” [HMH93]. Additionally, to favor either of the two traits runs a risk that the other does not acquire adequate resources for success. This trade-off can be generalized to resource gain versus risk. Thus, the trade-off between resource gain and risk avoidance is relevant.

The behavior of the individual is described by the control variable  $u$ .  $u$  is defined as the proportion of time spent in the high-energy situation out of the total time. The state  $x$  of the individual is a measure of its resource level. Houston et. al give examples of  $x$  as fat reserves in a bird or total mass of a fish.

The mean increase of state  $x$  given control variable  $u$  is denoted  $\gamma(u, x)$ . Houston et. al [HMH93] assume the mean increase in  $x$  for an individual with control variable  $u$  is given by  $\gamma(u, x) = a(x)u - b(x)$  for some functions  $a(x)$  and  $b(x)$ .

Table 6. Notation

<b>Symbol</b>	<b>Definition</b>
$u(t)$	Control variable
$x(t)$	State of an individual
$\gamma(u, x)$	The mean increase in $x$ per unit time for an individual with control variable $u$ and $x$
$M(u, x)$	Probability of termination of an individual with control variable $u$ and state $x$
$u_{OPT}(x, t)$	Optimal value of $u$ given state $x$ and time $t$
$x^*(t)$	Optimal level of resource of an individual at time $t$
$u^*(t)$	Optimal control variable, given as $u_{OPT}(x^*(t), t)$
$u_G(x)$	Gilliam strategy given $x$
$R_0$	Net reproductive rate

Table 7. Biological Terminology

<b>Term</b>	<b>Definition</b>
Control variable	The fraction of time an individual spends in a high-risk situation out of the total time
State	The amount of resource an individual holds
Refuge	A habitat with a predation rate of 0
Gilliam Strategy	Control variable $v \in [0, 1]$ such that $\frac{M(v, x)}{\gamma(v, x)} \leq \frac{M(u, x)}{\gamma(u, x)}$ for all $u \in [0, 1]$

The exact form and interpretation of  $a(x)$  and  $b(x)$  are dependent upon the individual and its situation [HMH93]. However, possible values of  $a(x)$  are limited by the fact that  $a(x) > 0$  for all values of  $x$ ;  $b(x)$  can be positive or negative.

$$\gamma(u, x) = a(x)u - b(x) \tag{4.25}$$

We can see this when we examine two environments 0 and 1. Let  $g_0(x)$  be the gain in Environment 0, and let  $g_1(x)$  be the gain in Environment 1. Suppose also that  $g_1(x) > g_0(x)$  so that Environment 0 has higher risk and reward than Environment 1. Assume there is an individual that travels between these two environments such that this individual has control variable  $u$ . Then,

$$\gamma(u, x) = (1 - u)g_0(x) + ug_1(x) \tag{4.26}$$

$$= (g_1(x) - g_0(x))u + g_0(x), \tag{4.27}$$

which is of the same form as (4.25). Thus,  $\gamma(u, x)$  is linear in  $u$ , but not necessarily in  $x$ .

The function  $M(u, x)$  denotes the mortality rate in this model. It is assumed that  $M(u, x)$  is an increasing function of  $u$  for fixed  $x$ . That is,  $M(u, x)$  increases when  $u$  increases and  $x$  remains constant. Houston et. al do not make any further constraints on  $M(u, x)$  but instead present multiple possible relationships between  $M$  and  $u$ . They consider a linear relationship, a strictly convex relationship, and multiple types of piecewise relationships. In particular, they stress the existence of

strictly convex graphs of  $M$  that have refuges. The authors refer to a *refuge* as “a special habitat in which the animal is safe from predators” [HMH93].

For example, suppose there is a bird with a choice between foraging ( $u = 1$ ) and vigilance ( $u = 0$ ). In certain habitats, the probability or rate of predation still exists even when the bird spends all its time in a state of vigilance [HMH93]. That is,  $M(0, x) > 0$ . A refuge is a third state  $s_3$ , which can in this case be envisioned as some physical space available to the bird that is not available to its predators. Because there are no predators in this state, the probability/rate of predation has value 0.

The authors denote the optimal strategy by  $u_{OPT}(x, t)$ .  $u_{OPT}(x, t)$  is a function that outputs the optimum strategy  $u$  given resource level  $x$  and time  $t$ . Furthermore, the functions  $x^*(t)$  and  $u^*(t)$  in order to describe the behavior of the individual over time.

The authors provide examples of two circumstances in which a trade-off between gain and risk can arise. An individual may require a certain level  $x$  of resource in order to reproduce, or it may require a certain amount of time  $T$  in order to reproduce [HMH93]. These two circumstances are known as fixed-state and fixed-time, respectively.

In determining the optimal strategy in a fixed-state situation in which the effect of time is not considered, Houston et. al [HMH93] refer to ‘Gilliam’s rule.’ [HMH93] and [Pit12] qualitatively describe this rule as minimizing the ratio of the mortality rate over the foraging rate. In [HMH93], this rule is expressed as the minimization of  $\frac{M}{\gamma}$ , and a function  $u_G(x)$  is defined such that  $u_G(x) = u$  such that  $\frac{M(u, x)}{\gamma(u, x)}$  is minimized.

In a fixed-state situation not taking the effects of time into account, the Gilliam Rule gives the optimal strategy [HMH93]. Here, as before, we denote the net reproductive rate of an organism as  $R_0$ .

**Theorem 4.2** (Adapted from [HMH93]).  *$u_{OPT} = u_G$  in a fixed-state situation without time constraints.*

*Proof.* In a fixed-state situation, suppose that the state level required for an organism to reproduce is  $x_0$ . By Theorem 4.1,  $R_0$  is maximized when  $\frac{\partial M}{\partial \gamma} = \frac{M}{\gamma}$ . Clearly, the probability of reaching  $x$  is maximized when  $R_0$  is maximized. Recall that  $\frac{\partial M}{\partial \gamma} = \frac{M}{\gamma}$  when  $\frac{M}{\gamma}$  is minimized. Then, the probability of reaching  $x$  is maximized when  $\frac{M}{\gamma}$  is minimized. Therefore,  $u_{OPT} = u_G$ .  $\square$

The  $\frac{M}{\gamma}$  rule is applicable to the motion of sunfish as they develop, the timing of metamorphosis in amphibians, and the levels of fat carried by migrating birds [HMH93].

## CHAPTER V

### CONCLUSIONS

The resources living organisms have must be allocated to survival and reproduction, but how should these resources be divided? Over the previous three chapters, we have attempted to answer this question using the mathematics of life history theory. We introduced the basic mathematics in Chapter II, we have derived answers from the lifetime fecundity function in Chapter III, and we have derived answers from habitat choice in Chapter IV.

In Chapter II, we demonstrated that the positive correlations observed by some field researchers are not indications that survival and reproduction do not represent a trade-off. Rather, it is the fluctuations of the total energy which cause survival and reproduction to sometimes be positively correlated. When the total energy available to an organism is held constant, survival and reproduction are negatively correlated.

In Chapter III, we utilized the lifetime fecundity function to determine the optimal amount of resource to allocate to reproduction. This concept was first introduced with Roff's work [Rof84] on fish populations. We then connected the lifetime fecundity function to resource allocation by realizing that the individual fecundity function  $m(t)$  is a function of  $R(t)$  and that the probability function  $\ell(t)$  is a function of  $S(t)$ . We were able to find the optimal amount of resource to allocate to reproduction by maximizing the lifetime fecundity function.

In Chapter IV, we explored how time, rather than energy or food, might be allocated. We considered an organism with a choice of habitat: One habitat had a

high mortality rate and low growth rate, and the other had a low mortality rate with a high growth rate. We first showed how minimizing the ratio of the mortality rate over the growth rate maximizes the net reproductive rate of the organism; then, we proved that this is the optimal strategy for a fixed-state organism. In doing so, we found the optimal allocations of time to survival and reproduction.

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