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LIFE HISTORY TRADE-OFFS

Objectives

- Develop a spreadsheet model of annual versus perennial life history strategies for plants.
- Determine how adult survival and offspring survival affect the breeding success of plants.
- Evaluate how trade-offs in reproduction and survival affect population growth.
- For a given environment, determine the life history schedule that maximizes growth.

Suggested Preliminary Exercises: Age-Structured Matrix Models; Life Tables and Survivorship Curves

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INTRODUCTION

A sockeye salmon (*Oncorhynchus nerka*) is born in an Alaskan stream. It migrates to the ocean and spends several years there while it grows to reproductive size, and then journeys back to its natal stream to spawn. It lays hundreds of eggs (few of which will survive to reproductive age) and then dies. Foxglove (*Digitalis purpurea*) is a plant that flowers when it reaches a critical size (usually 2 years after it germinates), produces hundreds of seeds, and normally dies after setting seed. Human beings (*Homo sapiens*) have a typical life span of more than 65 years and can produce offspring when they are teenagers. Female humans typically produce a single offspring in each reproductive bout (multiple births, even twins, are relatively rare) and provide more than a dozen years of care for their young. These examples describe the life history of various species. If you've worked through a life table exercise, you've essentially charted an organism's life history.

  Ecologists describe a species in terms of its reproductive life history. Life history schedules address the following questions:

- At what age does reproduction start?
- How many offspring are typically produced in a single reproductive bout?
- How many reproductive bouts does an organism have in its lifetime?
- Does number of offspring produced vary with the adult's age?

Species that reproduce only once during their life have a **semelparous** life history strategy. Salmon are examples of semelparous species. The fecundity schedule

for such an organism would have zero for all age brackets except the age at which the reproduction occurs. Semelparous species can be early reproducers (produce offspring in their first year of life, such as many annual plants), or late reproducers (produce offspring after their first year of life, such as salmon). In contrast, **iteroparous** species reproduce several times in a lifetime. Maple trees, humans, and sea turtles are examples of iteroparous species.

To begin our discussion of life histories, let's assume that a hypothetical species has two age classes and that its life history can be shown with a Leslie matrix. Let's also assume that the second age class is a composite age class consisting of individuals of age 2 and any older individuals. This Leslie matrix has the form

$$A = \begin{bmatrix} F_1 & F_2 \\ P_1 & P_2 \end{bmatrix}$$

Remember that the top row of the Leslie matrix gives the fertility (F) of age class 1 and age class 2+ (which is a composite of 2-year-olds plus any older individuals). Let's assume that $F_1 = F_2 = 10$ individuals per individual per year. The bottom row of the Leslie matrix gives the survival probabilities, P. The left entry is the probability that an individual in age class 1 will survive to age class 2+, and the right entry is the probability that an individual in age class 2+ will survive to live additional years, and remain in the 2+ age class. Let's assume that these parameters are 0.3 and 0.4, respectively. If we describe life histories generally in terms of early reproduction versus late reproduction and semelaparous versus iteroparous, we arrive at four life history strategies and their associated Leslie matrices (Table 1).

Table 1. Four Life History Strategies and their Associated Leslie Matrices

The top row of each matrix gives the fertility of age classes 1 and 2+, F_1 and F_2, respectively. The lower row of each matrix gives the respective survival probability for each class, P_1 and P_2. The left-hand column represents age class 1, the right-hand column age class 2+.

	Semelparous	Iteroparous
Early reproduction	$A = \begin{bmatrix} 10 & 0 \\ 0 & 0 \end{bmatrix}$	$A = \begin{bmatrix} 10 & 10 \\ 0.3 & 0.4 \end{bmatrix}$
Delayed reproduction	$A = \begin{bmatrix} 0 & 10 \\ 0 & 0 \end{bmatrix}$	$A = \begin{bmatrix} 0 & 10 \\ 0.3 & 0.4 \end{bmatrix}$

## *Trade-Offs between Reproduction and Survival*

Ideally, a species would reproduce as often as possible, have as many young as possible to maximize lifetime reproduction, and live forever. But is it that simple? An organism has a finite amount of energy to allocate to survival and reproduction. Energy allocated to reproduction means that less energy may be allocated to growth or maintenance (i.e., tasks that enhance survival). This creates a **trade-off** between present reproduction and survival, since organisms cannot maximize both. If size confers a significant survival advantage, for example, an organism may maximize its growth at the expense of reproducing until it reaches a critical size (Silvertown and Dodd 1999). And individuals that invest heavily in early reproduction may have poor survivorship later in life (Gotelli 2001). Figure 1 shows such a trade-off. The *x*-axis gives the proportional effort invested in reproduction, ranging between 0 and 1. The *y*-axis gives the survival rate, adjusted for the reproductive effort. When the proportional reproductive

Trade-offs in Current Reproduction and Survival
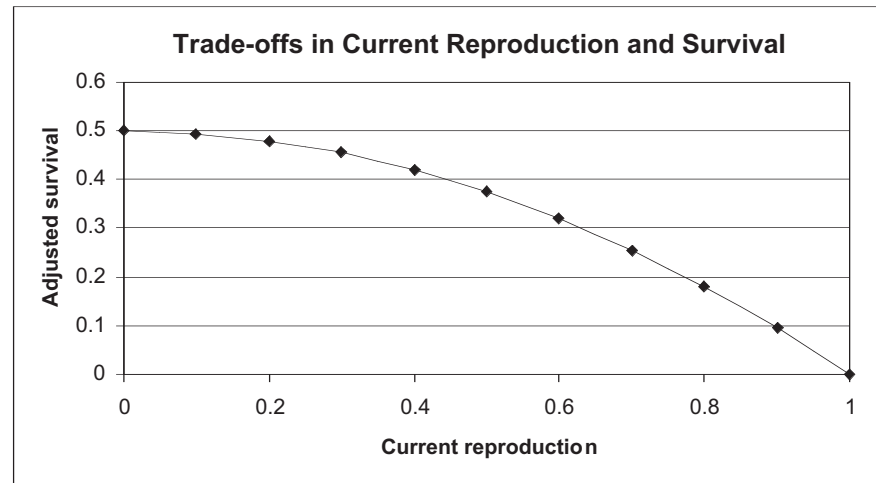
Figure 1   The shape of this curve indicates that virtually any energy devoted to reproduction will negatively impact survival; this species has a "high cost of reproduction" since the curve slopes downward.

effort is 0, no energy is devoted to current reproduction, and survival is determined by the intrinsic qualities of the environment in which the organism lives. In Figure 1, the survival rate is 0.5 even when individuals do not reproduce. When reproductive effort is greater than 0, it has a negative impact on survival, and the nature of this impact depends on the shape of the curve. When the effort is 1, all energy is devoted towards current reproduction, and survival becomes 0. Figure 1 has a fairly steep slope, which suggests that there is a "high cost of reproduction" in this environment. A high cost of current reproduction negatively impacts survival, which in turn affects future population size and hence future reproduction.

Figure 2 also shows trade-offs between survival and reproduction. However, survival is not decreased until almost all energy is devoted towards current reproduction. This environment would be considered a "low cost of reproduction" environment. Such environments may be so benign that resources are available for both survival and reproduction (survival is high no matter how much energy is devoted to reproducing). Or,

Trade-offs in Current Reproduction and Survival
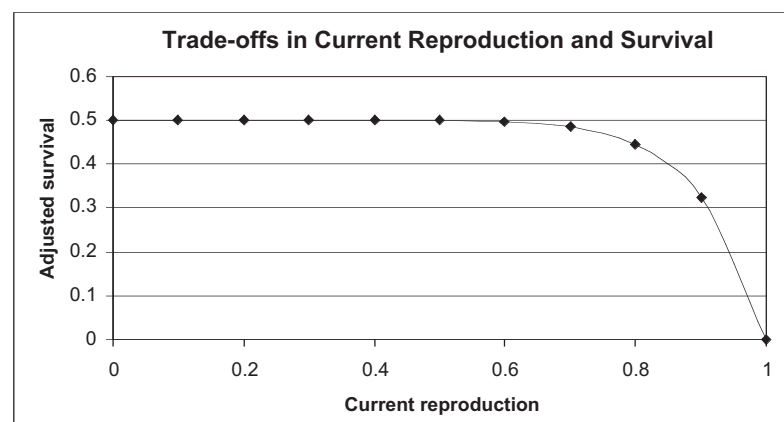
Figure 2   The shape of this curve indicates that energy expended on reproduction has little impact on survival unless almost all of an individual's energy is devoted to reproduction. This species has a "low cost of reproduction."

conversely, it may be that individuals die no matter how much effort is put into repro-duction (survival is low no matter how much energy is devoted to reproducing). For example, if breeding ponds dry out in the summer, all the adults die regardless of their reproductive effort.

Given such trade-offs, natural selection will "favor" those individuals whose life his-tory schedules maximize the number of offspring an individual contributes to the next generation, and select against individuals whose life histories are less compatible with the environment. The study of trade-offs in survival and reproduction, and how life his-tory strategies can evolve, is called **life history theory**. One such life history theory is the theory of *r-K* **selection** (MacArthur and Wilson 1967; Pianka 1970). This theory describes organisms as being *r*-selected versus *K*-selected, where the terms *r* (the instan-taneous rate of increase) and *K* (the carrying capacity of the environment) come from the logistic growth model (see Exercise 8, "Logistic Population Models"). Organisms that are *r*-**selected** live in highly disturbed environments, tend to increase in numbers exponentially with a high *r*, and then are depressed dramatically in numbers when a disturbance such as a storm or drought occurs. In other words, their growth is governed by *r* (or λ) until a disturbance occurs. Such populations rarely approach *K* and intraspe-cific competition has a negligible impact on growth rates. Because the future is uncer-tain in terms of resources, these organisms tend to breed early in life, are semelparous, and have large clutches.

In contrast, organisms that live in more stable, competitive environments are called **K-selected** species because their population numbers tend to be stable over time and exist at levels near the carrying capacity of the environment. Intraspecific competition is great for such species. These organisms tend to bear fewer offspring later in life and are iteroparous, because this schedule gives young a competitive advantage to survive in a competitive environment. A summary of how life history attributes are expected to vary for *r* and *K* selected species is given in Table 2.

Cole's Paradox

Even before *r-K* selection theory was formulated, Lamont Cole (1954) wondered about how life histories evolve in plant species. An **annual** plant is one that reproduces in its first year and then dies. Thus, an annual has a semelparous reproductive strategy. A **perennial** plant may also reproduce in its first year, but survives into future years and reproduces each year thereafter; thus it has an iteroparous reproductive strategy.

Cole realized that an annual strategy could achieve the same growth rate (λ) as a peren-nial strategy, where a perennial is immortal (never dies; survival = 1), as long as the annual can reproduce just one more offspring per year than the perennial. If we assume a pop-ulation is censused with a prebreeding census (all individuals are counted immediately before the birth pulse occurs, Figure 3), this means that an annual with a Leslie matrix **A** produces the same finite rate of increase (λ) as a perennial with Leslie matrix **B**:

$$\mathbf{A} = \begin{bmatrix} 11 & 0 \\ 0 & 0 \end{bmatrix} \qquad \mathbf{B} = \begin{bmatrix} 10 & 10 \\ 1 & 1 \end{bmatrix}$$

Note that in matrix **A** (the annual), reproduction occurs in only one age class (semel-parous), and that the probability of survival beyond age class 1 is 0, so individuals reproduce and then die. Matrix **B**, in contrast, shows reproduction occurring in both age groups (iteroparous), and survival equals 1. Since the two matrices yield the same λ, a perennial that produces 10 offspring per year and lives forever has the same fitness as an annual that produces just one more offspring and then dies. Cole wondered why we see perennial life history strategies at all, given that just a bit more reproductive effort could compensate for energy that otherwise would be devoted to survival. This is called **Cole's paradox**.

The key to understanding Cole's paradox is to realize that in a matrix model, the fertility rates for each age class (F_i for age class *i*) are the birth rates (b_i) adjusted for survival (see Exercise 13, "Age-Structured Matrix Models"). Figure 3 illustrates this using

Table 2. Summary of *r*- versus *K*-Selected Life History Strategies	
r-Selected	*K*-Selected
Reproduce early, since disturbance is frequent and unpredictable; those individuals that wait to reproduce may die before reproduction occurs.	**Reproduce later**, since individuals that reproduce early are likely to have smaller, less competitive offspring.
Produce many offspring per reproductive bout. Saving energy for future reproduction is fruitless if the probability of mortality in the future is uncertain.	**Produce fewer offspring** per reproductive bout, since fewer offspring with parental care are more likely to survive in a competitive environment than many offspring with no parental care.
Produce small offspring, because if there is a finite amount of energy that can be used for reproduction, more offspring can be produced if each offspring is small.	**Produce large offspring**, since smaller offspring will not be able to compete and survive in competitive environments as well as larger offspring.
Smaller adults. Because individuals breed at an early age, breeding individuals may be smaller on average than *K*-selected species.	**Larger adults** able to produce larger offspring.
Tendency is to reproduce once, then die. Allocating energy for future reproduction in an uncertain environment may lead to fewer offspring overall.	**Tendency to reproduce repeatedly**, because only one or few offspring are produced per reproductive bout and require care. Repeated reproduction allows more total offspring to be produced, spread out over the reproductive portion of the life cycle.
Type III survivorship curve. Because the environment is unpredictable, and because offspring are small, survivorship is low for young and intermediate ages.	**Type I survivorship curve**. Because the young are large and competitive, there is high survivorship of young and intermediate ages, then a drop-off as old age sets in.

Summarized from Begon et al. (1986).
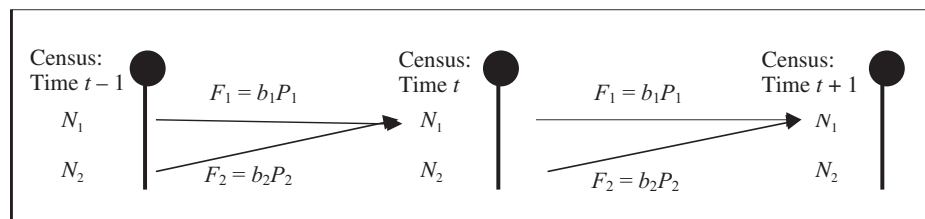
Figure 3   In this hypothetical population, the number of individuals of each age class (N_1 and N_2) is counted during the census, and a birth pulse (filled circles) occurs just after the census. Offspring are produced according to the birth rate (b_1 or b_2). Both age classes contribute individuals to age class 1 in the next year. However, in order for these young to be counted in the population as 1-year-olds (and to reproduce) in the next time step, they must survive almost a full year, until the next birth pulse. Thus, the fertilities are multiplied by the probability that an individual will survive to reproduce the following year (P_1 or P_2). The resulting adjusted fertility (b_iP_i) gives the number of offspring produced per individual that will survive and be counted in the next time step (Caswell 1989).

a hypothetical population with two age classes, censused over a 3-year period (time $t-1$, time t, and time $t+1$). Cole's paradox relies on the unlikely assumption that *all* individuals born in year t will survive to year $t+1$ (i.e., $P_1 = 1$).

Model Development

In this exercise, you will set up a matrix model of Cole's paradox, and will explore the conditions that lead to iteroparity, semelparity, early reproduction, and late reproduction. Our model will take the form of a Leslie matrix model, but will include something that Cole did not consider: trade-offs in survival and reproduction. The standard matrix model has the form

$$\begin{bmatrix} F_1 & F_2 \\ P_1 & P_2 \end{bmatrix} \times \begin{bmatrix} N_{1(t)} \\ N_{2(t)} \end{bmatrix} = \begin{bmatrix} N_{1(t+1)} \\ N_{2(t+1)} \end{bmatrix} \qquad \text{Equation 1}$$

where F_1 and F_2 are the fertility rates of 1-year-olds and 2-year-olds, respectively, and P_1 and P_2 are the survival rates. P_1 gives the probability that an individual in the first age class will survive to the second age class. P_2 gives the probability that an individual in the second age class will survive but remain in age class 2+. The model multiplies the matrix of fertilities and survivals by the number of individuals in each age class at time t to give the number of individuals in each age or stage class at time $t+1$. For example, the number of individuals in age/stage 1 at time $t+1$ ($N_{1(t+1)}$) is computed as

$$N_{1(t+1)} = F_1 \times N_{1(t)} + F_2 \times N_{2(t)}$$

The number of individuals in age/stage 2 at time $t+1$ is computed as

$$N_{2(t+1)} = P_1 \times N_{1(t)} + P_2 \times N_{2(t)}$$

We will modify the standard matrix model by adding terms to the F_i and P_i elements in the Leslie matrix, which control trade-offs in survival and reproduction (after Cooch and Ricklefs 1994).

$$\begin{bmatrix} F_1 \times E & F_2 \times E \\ P_1 \times (1-E^z) & P_2 \times (1-E^z) \end{bmatrix} \times \begin{bmatrix} N_{1(t)} \\ N_{2(t)} \end{bmatrix} = \begin{bmatrix} N_{1(t+1)} \\ N_{2(t+1)} \end{bmatrix} \qquad \text{Equation 2}$$

The term E gives the proportional effort of energy allocated towards current reproduction, and ranges from 0 to 1. Thus, the fertility rates are multiplied by E in the modified Leslie matrix. When $E = 1$, all energy is allocated toward current reproduction, so individuals reproduce with fertility rates in the standard model. As E decreases, the current fertility rate decreases proportionately. The trade-off between current reproduction and survival is reflected in the second row of the Leslie matrix. Each survival probability is multiplied by the term $(1 - E^z)$. The survival probabilities are adjusted depending on both E (the proportional investment into reproduction) and z (the environment's cost of reproduction). The lower the value of z, the higher the cost of reproduction (Figure 1), and the higher the z, the lower the cost of reproduction (Figure 2).

PROCEDURES

With this background in mind, let us begin with the model. The goal of the model is to explore how λ, the finite rate of increase, can be maximized given trade-offs in survival and reproduction, and to think about the kinds of environments that promote early versus late reproduction, and semelparous versus iteroparous reproduction. If you are rusty on Leslie matrices, refer back to Exercise 13 before you begin. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Model Cole's paradox.

1. Open a new spreadsheet and set up headings as shown in Figure 4.

	A	B	C	D	E
1	*Life History Trade-offs*				
2					
3					
4					
5		Age			
6		1	2+	*n*	
7		11	0	10	
8	**A =**	0	0	0	
9					
10	Numbers over time - no trade-offs				
11	Time	Age 1	Age 2	Total pop	λ

Figure 4

2. Enter the parameter values shown in cells B7–C8.

We will consider a plant that has just two age/stage classes. The matrix of cells

$$\begin{bmatrix} 11 & 0 \\ 0 & 0 \end{bmatrix}$$

is the life history for an annual plant. Each plant in the first year of life produces 11 offspring, and then dies. P_1, the probability that a individual in age class 1 will move to age class 2, is 0. Thus, F_2 and P_2 are also 0.

3. Enter the initial vector of abundances as shown in cells D7 and D8.

The initial vector of abundances $\begin{bmatrix} 10 \\ 0 \end{bmatrix}$

gives the starting number of individuals in age class 1 and age class 2+, respectively.

4. Set up a linear series from 0 to 50 in cells A12–A62.

Enter 0 in cell A12.
Enter **=1+A12** in cell A13. Copy cell A13 down to cell A62.
This will allow us to track the dynamics of this plant species over 50 years.

5. Enter formulae in cells B12 and C12 to link the number of individuals in age classes 1 and 2 to the vector of abundances in cells D7 and D8.

Enter the formula **=D7** in cell B12.
Enter the formula **=D8** in cell C12.

6. Enter a formula in cell D12 to compute the total population size at time 0.

Enter the formula **=SUM(B12:C12)** in cell D12.

7. In cell E12, Compute λ for year 0 as $N_{(0)}/N_{(1)}$.

Enter the formula **=D13/D12** in cell E12. Your result will not make sense until you have computed the total population size in year 1.

8. Enter formulae in cells B13 and C13 to compute the number of individuals in age class 1 and 2 in year 1.

Enter the formula **=$B$7*B12+$C$7*C12** in cell B13 to compute the number of individuals in age class 1 in year 1.

Enter the formula **=$B$8*B12+$C$8*C12** in cell C13 to compute the number of individuals in age class 2+ in year 1.

Remember, the matrix calculations are

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix} \times \begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} ax+by \\ cx+dy \end{bmatrix}$$

9. Copy cells B13–C13 down to cells B62–C62.

10. Copy cells D12–E12 down to cells D62–E62.

This completes the 50-year projection of your population. Your spreadsheet should now resemble Figure 5.

	A	B	C	D	E
10		Numbers over time - no trade-offs			
11	Time	Age 1	Age 2	Total pop	λ
12	0	10	0	10	11
13	1	110	0	110	11
14	2	1210	0	1210	11
15	3	13310	0	13310	11
16	4	146410	0	146410	11
17	5	1610510	0	1610510	11
18	6	17715610	0	17715610	11
19	7	194871710	0	194871710	11
20	8	2143588810	0	2143588810	11
21	9	2.3579E+10	0	2.3579E+10	11
22	10	2.5937E+11	0	2.5937E+11	11

Figure 5

11. Graph the population numbers over time.

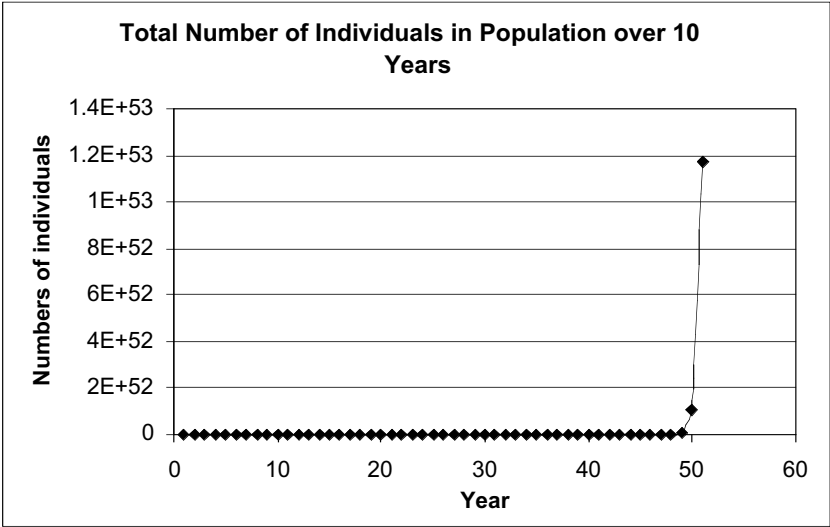Use the scattergraph option, and label your axes fully. Your graph should resemble Figure 6.

Figure 6

12. Change the matrix entries as shown in Figure 7.

	A	B	C	D
5		**Age**		
6		**1**	**2+**	***n***
7		10	10	10
8	**A =**	1	1	0

Figure 7

13. Update your projections (this may be done automatically, or by pressing F9).

The matrix entries now suggest an everlasting perennial. All individuals produce 10 offspring per year, and survival from age class 1 to age class 2+ is 1. Additionally, all individuals in age class 2+ survive with a probability of 1 to the next age class, and then survive with a probability of 1 to the next age class (and so on).

14. Answer Questions 1–3 at the end of this exercise.

15. Save your work.

B. Establish trade-offs for survival versus reproduction.

Now we will add trade-offs between survival and current reproduction into the model.

1. Set up new headings as shown in Figure 8.

We will let E be a proportional reproductive effort. If E is 1, then the organism reproduces at fertility rates given in the original Leslie matrix. If E is 0, then current reproduction is 0 times the fertility rates in the Leslie matrix. If E is any value between 0.1 and 0.9, that number is multiplied by the fertility rates in the Leslie matrix. Thus, E "brakes" the fertility rates by a proportional amount.

	K	L
6	**Trade-off parameters**	
7	***E =***	
8	***z =***	2
9	***P =***	0.5
10	***E***	**Adjusted survival**
11	0	
12	0.1	
13	0.2	
14	0.3	
15	0.4	
16	0.5	
17	0.6	
18	0.7	
19	0.8	
20	0.9	
21	1	

Figure 8

2. Enter 0.5 in cell L9.

P is a generic survival value, or the probability that an organism of age *x* will survive to the next time step. For now *P* = 0.5. You will be able to change this shortly.

3. Enter 2 in cell L8.

The variable *z* controls the cost of reproduction in an environment. For our purposes, we will let *z* range between 0 and 20. The higher the *z*, the lower the cost of reproduction, and the lower the *z*, the higher the cost of reproduction in a given environment. Currently *z* = 2, so the cost of reproduction is high. You will be able to see how *z* and *P* affect trade-offs in survival and reproduction shortly.

4. In cells L11–L21, enter an equation to compute adjusted survival for a given level of *E*. Refer to Equation 2.

Enter the formula **=$L$9*(1-K11^$L$8)** in cell L11. Copy the formula down to cell L21. The adjusted survival can be computed as $P \times (1 - E^z)$.

5. Graph the adjusted survival as a function of *E*.

Use the scatterplot option and label your axes fully. Your graph should resemble Figure 9.

Trade-offs in Current Reproduction and Survival

(y-axis: Adjusted survival, x-axis: Current reproduction)

Figure 9

6. Interpret your graph fully.
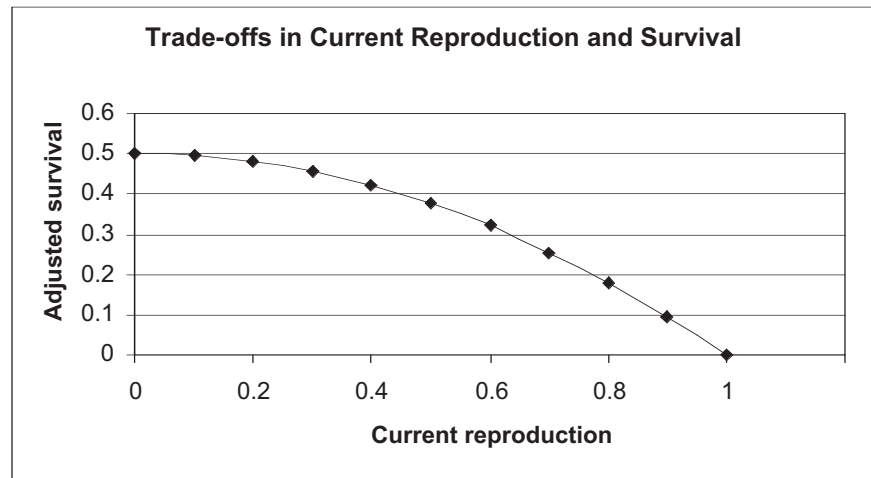
Keep in mind that this figure is for *z* = 2 and *P* = 0.5. This figure will change as you modify *z* and *P* in the next step. When current reproductive effort is 1 (100%), survival becomes 0 because all energy is devoted to reproduction. When current reproduction is 0, adjusted survival is at 0.5, the baseline survival value. In between, as current reproduction effort is increased, the adjusted survival probability decreases rather abruptly. This is the trade-off between energy allocated to survival and energy allocated to reproduction. We will incorporate this trade-off into the matrix model in Part C.

7. Increase the value of *z* to 20 by units of 5, and interpret your final graph (*z* = 20).

Your graph should resemble Figure 10.
You should see that as *z* increases, the cost of reproduction is lessened. When *z* is 20, there is still a trade-off between survival and reproduction, but survival is adjusted only when reproductive effort is close to 100% effort (*E* = 1). Habitats with high *z*'s are low cost of reproduction habitats.
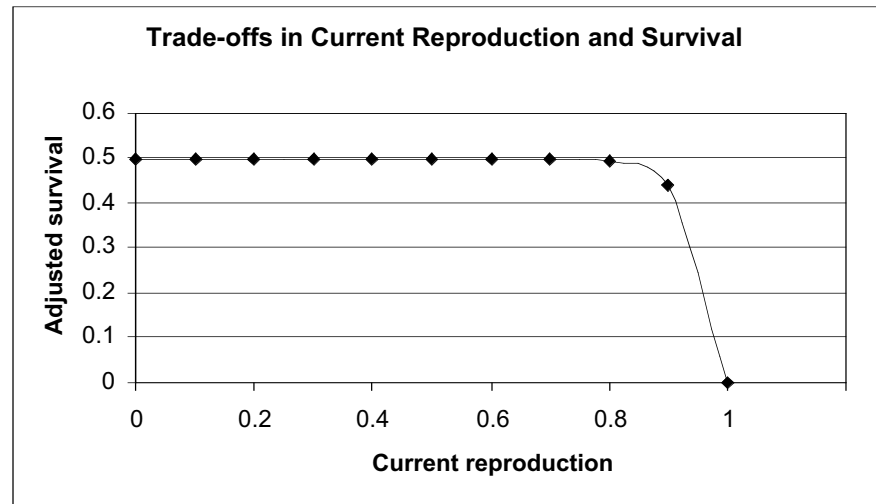
Figure 10

8. Save your work.

Now that you have a handle on how E and z function, the next step is to incorporate E and z in the matrix model.

C. Set up the trade-off model.

1. Set up new headings as shown in Figure 11.

	F	G	H	I	J
1			**Trade-off Model**		
2					
3					
4					
5			**Age**		
6		**1**	**2+**	*n*	
7		11	0	10	
8	**A =**	0	0	10	
9					
10			**Numbers over time - with trade-offs**		
11	**Time**	**Age 1**	**Age 2**	**Total population**	λ

Figure 11

2. Set up a time series from 0 to 50 in cells F12–F62.

Enter 0 in cell F12.
Enter the formula **=1+F12** in cell F13. Copy this formula down to cell F62.

3. Enter a formula in cells G12 and H13 that links to the initial vector of abundances in cells I7 and I8.

Enter the formula **=I7** in cell G12.
Enter the formula **=I8** in cell H12.

4. Enter a formula in cell I12 to compute the total population size. Compute λ in cell J12.

Enter the formula **=SUM(G12:H12)** in cell I12.
Enter the formula **=I13/I12** in cell J12.

5. Enter 0.5 in cell L7 and 2 in cell L8. *E* and *z* establish the cost of reproduction on survival for the trade-off matrix model.

	K	L
6	**Trade-off parameters**	
7	***E* =**	0.5
8	***z* =**	2

Figure 12

6. Enter formulae in cells G13–J13 to project population sizes in year 1, including trade-offs in survival and reproduction.

Our trade-off matrix has the form

$$\begin{bmatrix} F_1 \times E & F_2 \times E \\ S_1 \times (1-E^z) & S_2 \times (1-E^z) \end{bmatrix} \times \begin{bmatrix} N_{1(t)} \\ N_{2(t)} \end{bmatrix} = \begin{bmatrix} N_{1(t+1)} \\ N_{2(t+1)} \end{bmatrix}$$

Enter the formula **=$G$7*$L$7*G12+$H$7*$L$7*H12** in cell G13.
Enter the formula **=$G$8*(1-$L$7^$L$8)*G12+$H$8*(1-$L$7^$L$8)*H12** in cell H13.
Enter the formula **=SUM(G13:H13)** in cell I13.
Enter the formula **=I14/I13** in cell J13.

7. Copy cells G13–J13 down to row 62.

8. Graph the population size over time.

Use the scatterplot option and label your axes fully. Your graph should resemble Figure 13. What is the asymptotic λ for your model? (This is a key model output that will be compared to the models.)
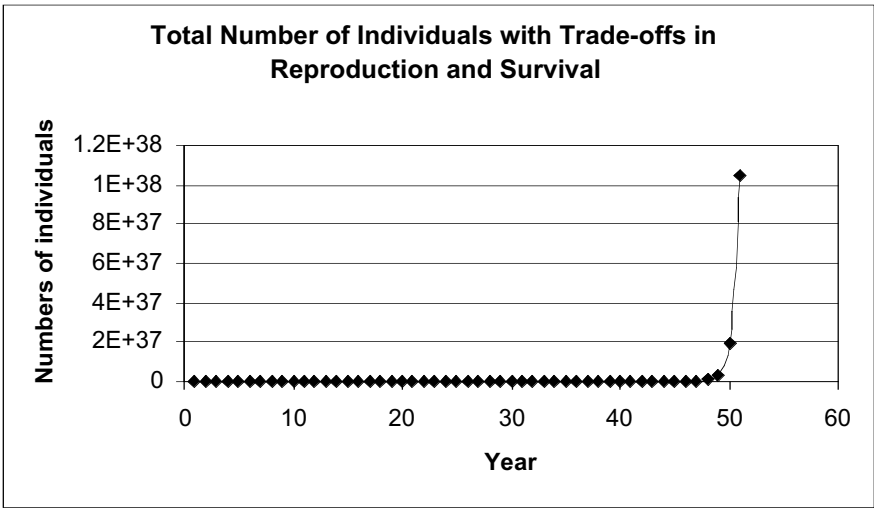

Figure 13

9. Save your work and answer questions 4–9.

QUESTIONS

1. What is Cole's paradox? Which of the two strategies (annual or perennial) is the fittest in this environment? Try entering other fertilities in the Leslie matrix so that the annual has 1 more offspring than the perennial. Does Cole's paradox still hold?

2. In modeling Cole's paradox, we set adult survival of perennials to 1 so that a perennial never dies. What is another major assumption of Cole's paradox regarding the fertility rates of the annual life history strategy?

3. To understand Cole's paradox more fully, it's helpful to break apart the F entry for age class 1 into its components, b_1 and P_1, where b_1 is the per capita birth rate of one-year-old females and P_1 is the probability that an offspring produced will survive to be counted as a one-year-old in the next census. Set up column headings as shown, and enter a formula in cell B7 to compute F_1 as cell B3*B4, or $b_1 P_1$. When the probability of juvenile survival decreases, how much must b_1 increase (cell B3) to match the λ of the everlasting perennial? Track your results for $P_1 = 0.1$ to 1 in increments of 0.1, display your results graphically, and interpret your results.

	A	B	C
3	$b_1 =$	11	
4	$P_1 =$	1	
5		Age	
6		1	2+
7		11	0
8	A =	0	0

4. In question 3, you addressed what b_1 must be for an annual to match the growth rate of an everlasting perennial when juvenile survivorship (P_1) is not 1. Now let's focus on what happens when a perennial is not immortal, and consider trade-offs between current reproduction and future survival. In the trade-off model, which of the strategies below will yield the highest asymptotic growth rate, λ: the annual matrix, **A**, or the perennial matrix, **B**? Explain your results.

$$\mathbf{A} = \begin{bmatrix} 11 & 0 \\ 0 & 0 \end{bmatrix} \qquad \mathbf{B} = \begin{bmatrix} 10 & 10 \\ 1 & 1 \end{bmatrix}$$

5. How does changing z in Question 4 affect the asymptotic growth rate, λ, for the annual? For the perennial?

6. Set up spreadsheet parameter values as shown below. Is this a low or a high cost-of-reproduction environment? Assuming a hypothetical organism that can produce 100 offspring maximum per year, what kind of reproduction schedule (early versus late, iteroparous versus semelparous) will maximize λ? Given your results, how can adjustments to E affect which life history strategy will be most fit?

	F	G	H	I	J	K	L
5		Age					
6		1	2+	*n*		Trade-off parameters	
7				10		$E =$	0.9
8	A =	0.1	0.1	10		$z =$	20
9						$P =$	0.1

7. Change the survival rates to 0.9 in your matrix. Would an early semelparous or early iteroparous strategy be favored under these conditions? Why?

	F	G	H	I	J	K	L
5		Age					
6		1	2+	*n*		Trade-off parameters	
7				10		$E =$	0.9
8	A =	0.9	0.9	10		$z =$	20
9						$P =$	0.9

8. Consider another environment and a different organism. Set up your spread-sheet as shown below. Assuming that your organism can produce a maximum of 5 offspring per year, what kind of reproductive schedule will maximize λ?

	F	G	H	I	J	K	L
5		**Age**					
6		**1**	**2+**	***n***		**Trade-off parameters**	
7				10		***E =***	0.5
8	**A =**	0.9	0.9	10		***z =***	1
9						***P =***	0.9

9. Suppose an organism's life history can be described with the Leslie matrix shown below. What level of E will produce the highest λ? Explain your result in detail in terms of trade-offs in reproduction and survival. What level of E would produce the highest λ if cells G8–H8 = 0.9? Explain.

	F	G	H	I	J	K	L
5		**Age**					
6		**1**	**2+**	***n***		**Trade-off parameters**	
7		1	5	10		***E =***	0.6
8	**A =**	0.4	0.4	10		***z =***	1
9						***P =***	0.4

10. Two marine bivalves, *Mercenaria mercenaria* and *Gemma gemma*, live in the same habitat. However, their reproductive strategies are very different. *M. mercenaria* is a broadcast spawner, meaning that male and female adults release eggs and sperm into the water column where external fertilization takes place, and the larvae undergo planktonic development. *G. gemma* is a brooder, meaning females retain their eggs and fertilization is internal. The offspring undergo direct development within the female. *G. gemma* produce small broods during the reproductive season, while *M. mercenaria* releases thousands of gametes into the water column. Surprisingly, both species enjoy similar reproductive success. Let's assume that in each reproductive season *G. gemma* will successfully rear 25 offspring that survive to be counted as N_1 individuals, and *M. mercenaria* will release 4000 gametes, all of which will be fertilized. Assuming equal costs of reproduction, what must the survival rate of *M. mercenaria* offspring (P_1) be in order to equal the reproductive output *G. gemma*?

*11. (Advanced) Some organisms have life histories that cannot be described as either *r* or *K*. "Bet-hedging" is a strategy that is predicted to evolve in environments that have unpredictable disturbances that increase the mortality of young, but not adults. If young are produced all at once, and it turns out to be a bad year, then an adult's fitness is 0. But if young are spread out across different generations, fitness may be increased by producing at least some young in some years when conditions are good. Add an element of stochasticity to your model that affects juvenile survival rate either by letting F_1 vary stochastically, or by splitting apart F into its components b_1 and P_1 (as in Question 3) and letting each component vary. Adjust your model, then examine the life history conditions that are needed to maximize λ.

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