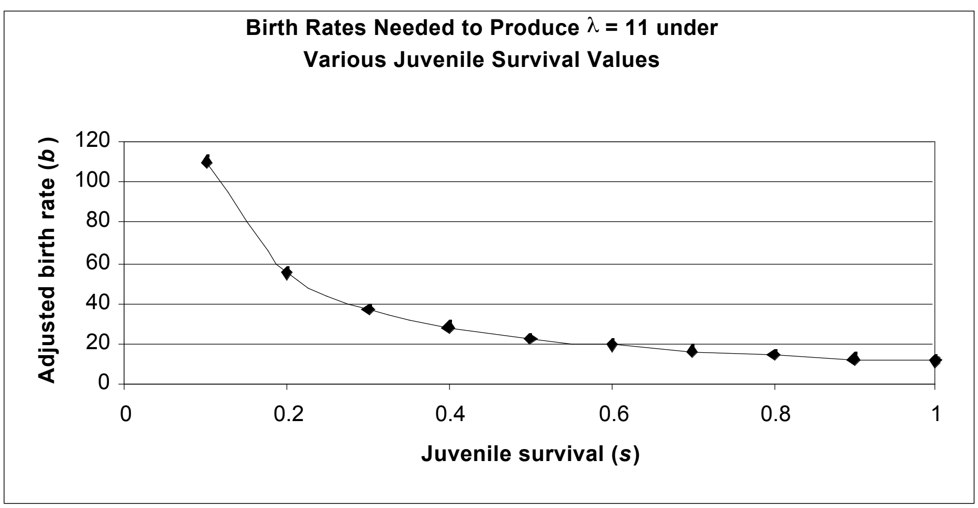
Answers to Exercise 35

Life History Trade-Offs

1. You should see that both strategies produce exactly the same λ over time. This is Cole's paradox: an annual that has a fertility rate that is just 1greater than an ever-lasting perennial will achieve the same finite rate of increase. This relationship holds with other matrix entries, as long as the annual fertility in year 1 is one greater than the perennial fertility in years 1 and 2. Both strategies are equally fit.

2. A hidden assumption is that all annuals that are born survive to reproduce. Since the matrix model discussed in the introduction relies on a pre-breeding census, we count 1 and 2 year-olds just before they breed. Thus, in order for all 11 offspring to be reproducing as adults, the survival rate of juveniles must be 1.

3. When the *F*'s are split into its component parts, b and s (survival of juvenile to year 1 census), Cole's paradox becomes clear: *s* must = 1 in order to match the λ of the everlasting perennial. When *s* is decreased, however, *b* must increase to maintain the λ at 11. This trade-off is not linear. When juvenile survival rates of juveniles are low, *b* must be much greater to compensate for juvenile mortality.



4. You should see that the perennial strategy yields a higher λ than the annual strategy given the matrices

$$A = \begin{bmatrix} 11 & 0 \\ 0 & 0 \end{bmatrix} \quad B = \begin{bmatrix} 10 & 10 \\ 1 & 1 \end{bmatrix}.$$

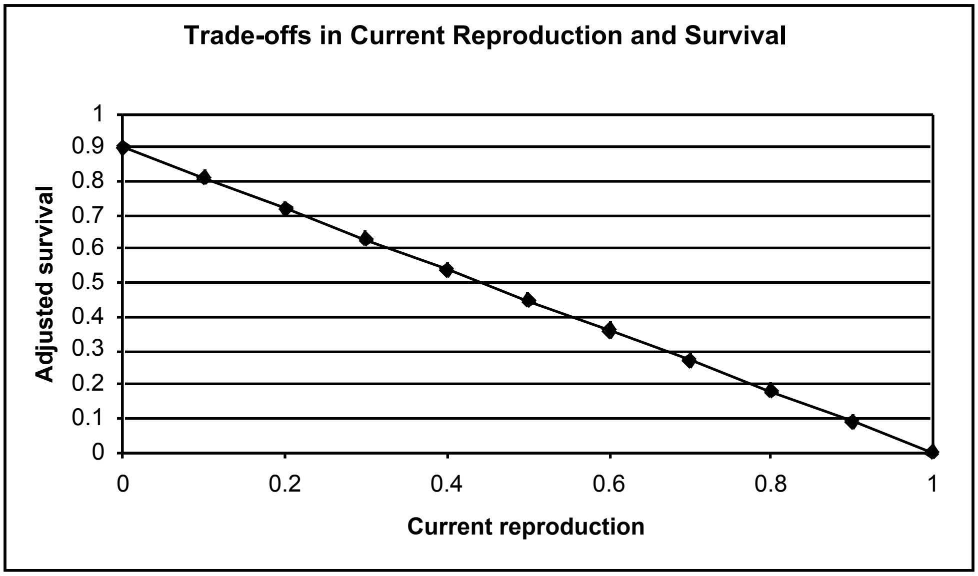
Matrix **A** has a finite rate of increase of 5.5, and Matrix **B** has a finite rate of increase of 5.75. The environment, as determined by the parameters E and z, drive the result. With $E = 0.5$ and $z = 2$, the environment has a fairly high cost of reproduction. This cost of reproduction affects P_1 and P_{2+}. It does not impact juvenile survival since this survival is incorporated into the fertility rates. Since annuals have P_1 and $P_2 = 0$, the result of the trade-off model for annuals is to reduce the fertility rate in half (because $E = 0.5$). This yields a $\lambda = 5.5$. For the everlasting perennial (matrix **B**), the trade-off reduces survival to 0.75 (see this for yourself by entering 1 in cell L9, and then examine the resulting adjusted survival for $E = 0.5$ in cell L16. Both P_1 and P_2 survival are reduced to 0.75 when the proportional effort invested in reproduction is 0.5. Although the survival was reduced, the perennial strategy still yields a greater λ than matrix **A** because fertility is adjusted to 5.0 (as opposed to 10). This combination of adjusted survival and fertility rates still yields a higher l than the annual, so this life-history genotype will increase in numbers over time.

5. This environment is a low cost of reproduction because survival is not impacted until almost all energy is allocated towards reproduction. The survival values, P1 and P2, suggest that the environment is harsh, and that all individuals (age 1 or age 2) have a low survival probability. Under these conditions, early reproduction is favored over late reproduction. Both iteroparous and semelparous schedules produce nearly identical lambdas (when $F_i = 100$). Given this result, an annual strategy in which $E = 1$ would increase l even further. When $E = 1$, P_1 and $P_2 = 0$, so a plant that puts all of its energy into reproduction and 0 into survival will be the most fit genotype.

6. The annual strategy will still lead to the highest λ, even in an environment that is reality benign. In this habitat, there is no cost to reproducing early (survival is not decreased substantially), and thus early reproduction does not affect future reproduction at all. When $F_1 = 100$ and $F_2 = 0$, $\lambda = 90$. When $F_1 = 100$ and $F_2 = 100$, $\lambda = 90.8$. A plant can increase λ further by allocating all of its energy towards reproduction ($E = 1$).

7. This environment has a very high cost of reproduction on survival. If individuals do not allocate energy towards reproduction, their survival rate is maintained at 0.9. If energy is allocated towards reproduction, survival decreases linearly with increases in reproductive effort. Under such conditions, the iteroparous reproductive schedule

leads to the highest λ.



8. In this situation, λ is maximized when E =0.7. Any more allocation towards reproduction results in fewer individuals in age class *2+* reproducing, and those individuals have the highest fertility rates. If survival rates were increased to 0.9, λ would be maximized at E = 0.5.