Notes on Life History Theory

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Broadly speaking the kinds of questions that are addressed in life history theory include how fast to grow, when to mature, when to reproduce, how many offspring to make, and why things senesce.

There are several different strategies we can take in developing models to address these questions. The simplest would be to simulate evolution directly by defining a population of individuals, specifying schedules of growth and maturation, births and deaths, any relevant trade-offs, and some scheme for mutation. These are the easiest to get going but are by far the hardest to interpret. With many parameters, it is difficult to evaluate the generality of a specific set of simulation results.

Somewhat more analytically tractable models arise from either a population / quantitative genetics framework. Again, we specify schedules and allow them to evolve but here we need an explicit measure of fitness. Given these we can write models for the evolutionary dynamics and numerically evaluate the end points.

Optimality-based models are among the easiest to analyze but this tractability is obtained at the cost of ignoring individual variation and evolutionary dynamics in order to ask the simplest question - what life history maximizes fitness. Note that we do not assume that any particular idividual is making optimal decisions. Instead, we ask what is the best that could be done under a given set of constraints in order to establish a baseline for comparison against what things actually do. This is the approach we will take. It is worth noting that in many cases, all of these approaches lead to the same conclusions.

To give you a sense of where we are going, here is an outline of where we are going (of course we might not get all the way there!)

Day 1

    a. How much energy should be invested per offspring?

    b. An aside on Population growth - scalar population in constant environment. Fitness in fluctuating environments.

   c. What conditions favor iteroparity v. semelparity? When recruitment (i.e. juvenile survival) is random?

Day 2

    a. Fitness in age-strucured populations: Lambda v. R0

    b. What is the optimal age at maturation? How does this change if lambda isn't 1?

    c. How fast should an individual grow?

    d. Why do things senesce?

Egg size - Egg number trade-off

Our first question is how much energy should a mother invest in each offspring? Assume that offspring survival (or fitness) is a function of the energy provided by the mother (call it x) and that a mother has a finite total amount of energy to be divide among some number of offspring.

To begin, we need to think about what a reasonable shape might be for the relationship between offspring survival ($S(x)$) and the energy invested. The easiest thing to do is start with the corners - We can be pretty sure that zero investment will yield 0 survival and that maximum investment will generate maximal survival, which will probably be less than 1.
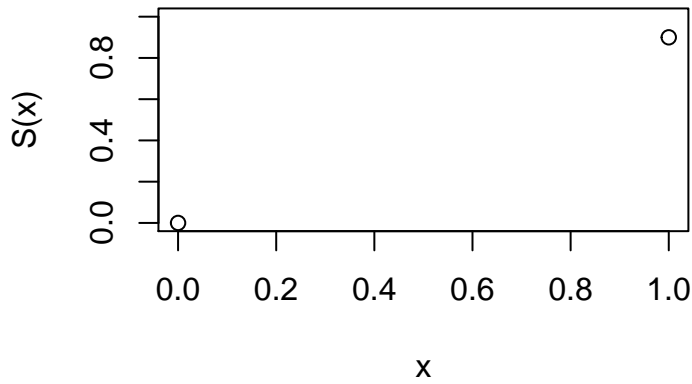
Now we need to think about how to connect those dots. Since eggs always cost something to make, even if they arent going to be particularly good (e.g. imagine the cost of making an egg that has everything except DNA), we migh argue that there should be some minimal investment below which survival is zero.

The other thing we migh argue is that the marginal benefit of additional energy is decreasing. That is, it is probably reasonable to assert that the change in survival obtained by going from 1 joule to 2 joules is bigger than the increment in survival going from 1000 to 1001. Mostly what this implies is that the curve should be flattening out to the right.

That gets us to here-
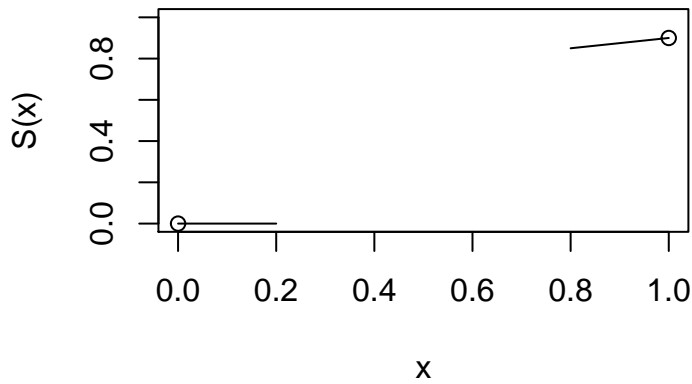
How we connect these segments is less clear, but let's just say there there's is some smooth curve that does it.
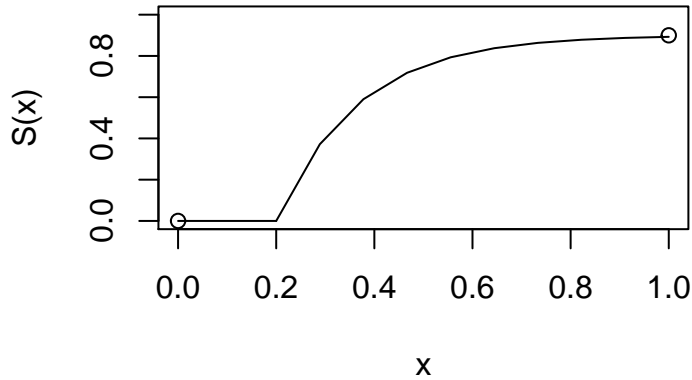
Now that we have a graphical model for how an offspring's survival increases with maternal investment, we need to write down an expression for maternal fitness. Let's say the mom is going to make n offspring and invest x in each. A reasonable assertion for the fitness that mom accrues through this round of reproduction would be

(1)
$$F = nS(x)$$

Next, let's say that the mom has E total units of energy which is divided evenly among the n offspring, i.e, $E = nx$.

Now, if we knew ahead of time that the mom is going to make 2 offspring, that would mean that $x = E/2$. But in the general case, both n and x are free to vary and we want to choose both such that fitness is maximized. But since E is fixed, we can reduce our 2-d problem back to 1 by making the substitution $n = E/x$ in our model for fitness, i.e. (1) which gives

$$F = \frac{E}{x}S(x)$$

Now, to find the optimal investment, we will take the derivative with respsect to x and set that equal to zero. Doing so, we get

$$\frac{dF}{dx} = \frac{E}{x}S'(x) - \frac{E}{x^2}S(x) = 0$$

where we've used $\frac{dS}{dx} = S'(x)$ to keep the notation tidy. We can simplify this by multiplying through by $-x/E$ to find that the optimal investment, x^* satisfies

(2)
$$S(x^*) - x^*S'(x^*) = 0$$

Now, it might seem like this is as far as we can go without specifying $S(x)$ but there's a bit more we can do. The trick is to make the analogy between (2) and the equation for a line. Recall the 'point-slope' formula for a line: $y = y_1 + m(x - x_1)$ Where y_1 is the height at the point x_1 and m is the slope.

For example, the line going through the point (1/2, 1/2) with a slope of 4/5 would look like
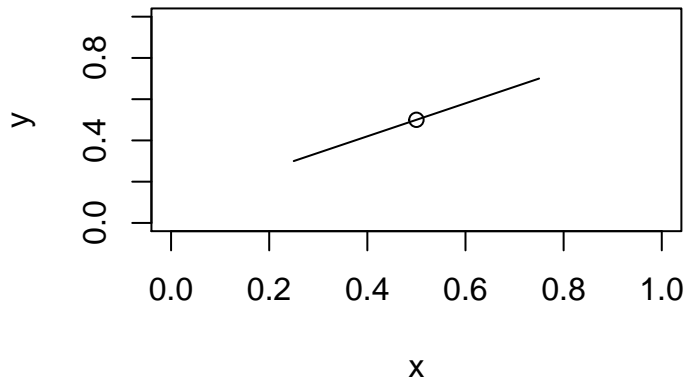
Now, let's return to our optimality condition (2) and try to make the analogy with the equation for the line. Recall that the derivative is the slope of the tangent line at x^* so that a line passing through $x^*, S(x^*)$ with slope $S'(x^*)$ would be $y = S(x^*) + S'(x^*)(x - x^*)$ We can plot this on our fitness graph-
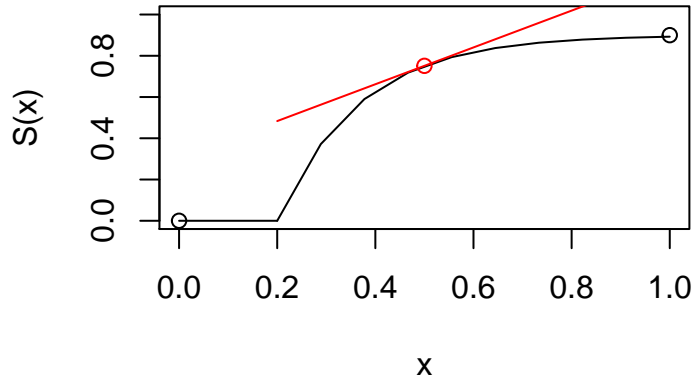
Comparing this linear equation with our optimality condition, we can see that when $x = 0$ optimality implies $y = 0$. That is, the optimal investment is where the tangent to S passes through the origin. In this particular graph, this happens at x^* 0.4)
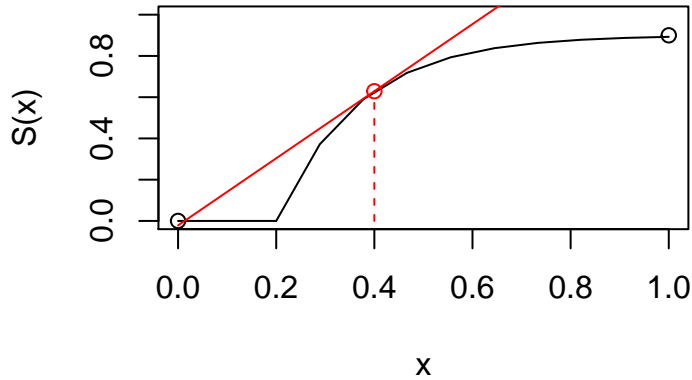
This analysis tells us a few things. Most importantly, it tells us that offspring will, generally speaking, be less than maximally fit. That is, the optimal investment by the mom is always going to be less than what it would take to make the 'best possible' offspring.

Second, since we never wrote down an explicit equation for $S(x)$, we will get more or less the same result for any survival / fitness function that has a) some minimal investment threshold and b) a negative second derivative (i.e is concave down). If there isnt a threshold, then the argument still works provided that the slope at the origin is less than 1 and there is an inflection point.

A brief aside on population growth

Before we tackle our next question in life history theory, let's review some important results on population growth. If we have a closed population without density dependence in which all reproducing individuals are identical, we can write the population dynamics as a recursion

(3)
$$N_{t+1} = \lambda N_t$$

where λ is the per capita growth. A solution to this recursion is given by

(4)
$$N_t = \lambda^t N_0$$

which is straightforward to verify by substituting into (3). If $\lambda = 1$ the population size doesnt change while the population size grows (shrinks) exponentially if λ is >1 (<1).

Now, consider what happens if we have two clones that are growing in this way, but with different per capita rates, say λ and ω for clones 1 and 2, respectively. If they start out at the same relative abundance, what can we say about the fraction of the total population that is clone 1, say π_t? Specifically, we can write

$$\pi_t = \frac{N_{1,t}}{N_{1,t} + N_{2,t}}$$

And plugging in our exponential growth equation (4) we get

$$\pi_t = \frac{\lambda^t N_0}{\lambda^t N_0 + \omega^t N_0}$$

which simplifies to

(5)

$$\pi_t = \left\{ 1 + \left(\frac{\omega}{\lambda} \right)^t \right\}^{-1}$$

So, if $\lambda > \omega$ then π_t goes to 1. From this it looks like the population will ultimately be entirely composed of clone 1. But, counter-intuitively, since we didnt say anyting about $\omega < 1$, clone 2 could be growing exponentially – even though it is becoming rare in the population.

Next, let's think about what happens when the environment is fluctuating, such that the growth rate for each year is allowed to vary. That is

(6)

$$N_{t+1} = \lambda_t N_t$$

The solution to this one isn't quite as pretty. In general it is given by

(7)

$$N_t = \prod_{i=0}^{t-1} \lambda_i N_0$$

Now, for simplicity, let's imagine that there are only two states - one in which growth is good and one in which it is bad, which we will label λ_g and λ_b, respectively. Since it doesnt matter we do the multiplication, we can re-write the product in terms of the number of years that the environment was good or bad, which we'll call t_g and t_b. That is

$$N_t = \prod_{i=0}^{t-1} \lambda_i N_0 = \lambda_g^{t_g} \lambda_b^{t_b} N_0$$

If t years have gone by, and we let p be the fraction of them that were good (i.e. $p = t_g/t$), then $t_b = (1 - p)t$. So we can re-write this one more time as

(8)

$$N_t = \lambda_g^{pt} \lambda_b^{(1-p)t} N_0 = \left(\lambda_g^p \lambda_b^{(1-p)} \right)^t N_0$$

The thing in parentheses is the geometric mean. So if we wrote $\lambda_{geo} = \lambda_g^p \lambda_b^{(1-p)}$, then (8) would have the form $N_t = \lambda_{geo}^t N_0$ which is the same form as (4). So the population eventually grows (or shrinks) exponentially at a rate given by the geometric mean. To make this a bit more concrete, lets think through what would happen if $\lambda_g = 1.3$ and $\lambda_b = 0.75$ and $p = 1/2$. The geometric mean is ~0.99. So even though the *average* growth rate is 1.025, the population will eventually go extinct.

Before we go on, it is worth noting that this works when there are more than two environments. To see this, let's re-write the geometric mean as

$$\lambda_{geo} = \left(\prod_{i=0}^{t-1} \lambda_i \right)^{\frac{1}{t}} = \exp \left[\frac{1}{t} \sum_{i=0}^{t-1} \ln \lambda_i \right]$$

and recognize that $\frac{1}{t} \sum \ln \lambda_i$ is the sample average of $\ln \lambda$ which converges to the 'population' mean in the limit of large t. So, regardless of how many values of λ there are, in the long run, the population size is determined by their geometric mean.

Now imagine again that we have two clones with different growth rates and are interested in which one will predominate in the long run. Without repeating the calculations above, we can just plug our geometric mean result for (8) into (5) to determine the long run fraction of the population that will be type 1. Following the same line of argument as before, the clone with the larger geometric mean will predominate. But what's interesting about this - and the reason to have gone through all this trouble - is that the geometric mean is

generally different (less than) the arithmetic mean. So we can have two populations with the same *average* growth rate but different geometric means (the one with the smaller variance in growth will have a higher geometric mean). In fact, we can have a population with a higher average growth, but lower geometric mean growth - can you guess which one will win?

Iteroparity v. Semelparity

One of the earliest topics addressed in life history theory is the question of why some species breed once and die (aka annual plants and semelparous animals) while others breed over many years (perennial plants and iterparous animals). The simplest versions of this problem start with a life cycle in which the current generation produces offspring (at per capita rate b) which have to survive until the next breeding season (with probability s_j), at which point they are mature. In the semelparous case, all of the current adults die, so that the population size at the next breeding season is simply

$$N_{t+1} = s_j b N_t$$

In the iterparous case, adults survive to the next breeding season with probability s_a so the next population size is

$$N_{t+1} = (s_j b + s_a) N_t$$

Obviously if $s_j b$ is the same for both semelparous and iteroparous genotypes, the iterparous type always dominates. Unless $s_a = 0$ in which case, they are semelparous anyway... So let's use b^* for the iteroparous type and assume that $b > b^*$. This makes sense if we imagine that in order to survive to the next breeding season, the iteroparous types must be holding something back from reproduction.

Comparing the population growth rates, we expect semelparity to evolve when $s_j b > s_j b^* + s_a$. Rearranging this, we get semelparity when $b - b^* > s_a/s_j$, that is, when the number of additional offspring that can be gained from semelparity exceeds the ratio of adult to juvenile survival. So we expect iteroparity to be more likely when juvenile survival is much lower than adult survival and vice versa.

We can also think of this as a trade-off problem. That is, we could focus on the iteroparous case and try to say something more specific about how reproduction affects adult survival. We will still model the population growth rate with the same equation, but say that s_a is some function of b, that is $\lambda = s_j b + s_a (b)$. If assume that $s_a (b)$ decreases with b then we have a trade-off; increasing b directly increases fitness (i.e. λ) at the expense of reducing future fitness through adult survival. The idea now is to ask what value of b would maximize fitness. Before we do this, let's try to think this through a bit more. What would a reasonable shape for $s_a(b)$ look like? What would this imply for fitness? It is worth your time to go through the exercise of drawing a few possibilities and thinking through their implications. I worked through two below-
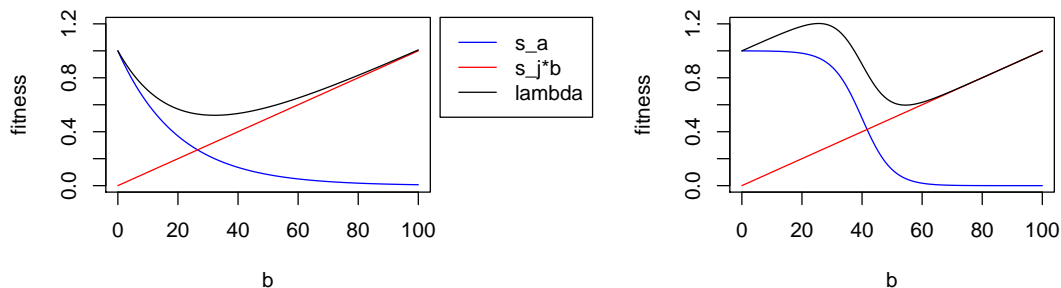
In both plots the blue line is the relationship between adult survival and fecundity. The red line is the gain in fitness from $s_a(b)$ and the black line is the sum of the red and blue lines, i.e. fitness. The main difference

between the plots is that on the right, there is a region over which a small investment in reproduction doesnt change survival much. The upshot is that in the scenario on the left, there is no hump in fitness! The optimal thing to do is to reproduce as much as possible at the expense of any possibility of survival. That is, the optimal strategy is to be semelparous. On the right, though, there *is* an internal maximum in fitness, at around $b = 25$. But if we think about it - the gain from additional reproduction (all the way on the right) is just going to keep increasing. So the optimal thing to do, depends on the range of feasible birth rates. If the maximal b is less than 100, the best thing to do is to be iteroparous: produce ~25 offspring and survive to next year. On the other hand, if there upper limit to fecundity is 200 or so, then semelparity is the way to go.

It might seem like this graphical approach lacks a bit of rigour. How can we be sure the conclusion we've reached is reasonable? Well, even without specifying an equation for $s_a(b)$ we can make some progress in this direction. We know that at the optimum, the first derivative of fitness needs to be 0 and the second derivative has to be negative. So let's work through that-

$$\lambda = s_j b + s_a(b)$$

$$\frac{d\lambda}{db} = s_j + \frac{ds_a}{db}$$

$$\frac{d^2\lambda}{db^2} = \frac{d^2 s_a}{db^2}$$

From this we can see that we need the second derivative of s_a to be negative, if we are going to have a maximum in fitness. This is the ingredient that is present in the drawing on the right and absent from the drawing on the left. What it means biologically is that in the vicinity of a fitness maximum, the decrease in survival with an increase in fecundity must be getting steeper.

Fluctuating Environments

So far, we've been thinking about this in terms of a constant environment. But what happens if the environment is fluctuating? Let's return to the comparison of the semelparous and iteroparous growth rates, but allow for the possibility that juvenile survival fluctuates from one year to the next. For simplicity we'll say that in a typical year the juvenile survival is σ and that every once in a while juvenile survival is reduced by some fraction, ϵ. More specifically, we'll say that $s_j(t)$ takes the value $\sigma(1-\epsilon)$ with probability p and is equal to σ otherwise. Let's leave everything else constant, so that the geometric mean growth rate for the semelparous case is $\lambda_{geo}^{sem} = [\sigma b]^{1-p} [\sigma(1-\epsilon)b]^p$ which simplifies to

$$\lambda_{geo}^{sem} = \sigma b \left(1 - \epsilon\right)^p$$

In the iteroparous case, the geometric mean growth rate is $\lambda_{geo}^{iter} = [\sigma b^* + s_a]^{1-p} [\sigma(1-\epsilon)b^* + s_a]^p$ which simplifies to

$$\lambda_{geo}^{iter} = [\sigma b^* + s_a] \left(1 - f\epsilon\right)^p$$

where $f = \sigma b^*/(\sigma b^* + s_a)$ which has to be between 0 and 1. Recall that the condition under which iteroparity is favored is given by $\lambda_{geo}^{iter} > \lambda_{geo}^{sem}$ which means

(9)
$$[\sigma b^* + s_a] \left(1 - f\epsilon\right)^p > \sigma b \left(1 - \epsilon\right)^p$$

To extract some insight from this, let's imagine that in a typical year the semelparous and iteroparous types have roughly equal fitness, i.e. $[\sigma b^* + s_a] \approx \sigma b$ so that (9) reduces to

$$(1 - f\epsilon)^p > (1 - \epsilon)^p$$

which is always true for $f < 1$ and $0 < p \leq 1$. This means that iteroparity is favored by fluctuating environments, even when the fluctuation is relatively rare or has a small effect on juvenile survival.

A brief digression on fitness in age-structured populations

Our previous models all implicitly assumed that all mature individuals were equal with respect to survival and fecundity. This is a handy simplification that alloed us to gain some nice insights, but it is hardly realistic. It is much more often the case that survival and fecundity vary with size or age. So let's think about how to characterize population growth in a populatio where this is true. To begin, let's use $N_{a,t}$ to indicate the number of individuals of age a that are present at time t, and let ϕ_a be the number of offspring an age a individual can produce. Then the number of newborn individuals at time t, say B_t, is given by

$$B_t = N_{1,t}\phi_1 + N_{2,t}\phi_2 + N_{3,t}\phi_3 + ...$$

Since we have not assumed a maximum possible age, the ... is there to indicate that the terms just keep going. Of course, the individuals who are age 1 in year t were born in year $t-1$ and survived to age 1. Likewise, individuals who are age 2 in year t were born in year $t-2$ and survived to age 2, etc. Let's let l_a indicate the probability that an individual survives to age a, so that we can write $N_{a,t} = B_{t-a}l_a$. Plugging this in, we get a *renewal* equation for B_t, i.e.

(10)
$$B_t = B_{t-1}l_1\phi_1 + B_{t-2}l_2\phi_2 + B_{t-3}l_3\phi_3 + ...$$

Now, to make the analogy with the previous models of population growth, we are going to guess that the population is growing exponentially (or at least that it will ultimately do so). If that's the case, then the numbers of individuals born at time t is going to be given by $B_t = \lambda^t B_0$ just like it was in our previous digression on population growth. Plugging this hypothetical solution into (10) everywhere we have a B we get

$$\lambda^t B_0 = \lambda^{t-1}B_0 l_1\phi_1 + \lambda^{t-2}B_0 l_2\phi_2 + \lambda^{t-3}B_0 l_3\phi_3 + ...$$

Let's tidy this up a bit by canceling B_0 and λ^t to get $1 = \lambda^{-1}l_1\phi_1 + \lambda^{-2}l_2\phi_2 + \lambda^{-3}l_3\phi_3 + ...$ which we can write even more compactly with a summation -

(11)
$$1 = \sum_{a=1}^{\infty} \lambda^{-a} l_a \phi_a$$

which is known as the Euler-Lotka equation. This equation defines fitness in an age-structured population. That is, fitness is given by the value of λ that makes the right hand side equal to 1. It would be nicer if we had an explicit formula for λ but, alas, in the general case this implicit solution is the best we can do.

Note that in a stable population, $\lambda = 1$ and the Euler-Lotka equation reduces to $1 = \sum l_a \phi_a$. This sum is the lifetime reproductive output, often denoted R_0. So in a stable population the lifetime production of offspring is 1. This makes sense, right? If, instead, over an individual's lifetime they made more than 1 offspring, the population would be growing.

Alot of the time, it is easier to work with R_0 than with λ in age-structured life history problems. It is not uncommon for theoreticians to assume that there's some unspecified mechanism holding the population steady in order to avoid the complications of working with λ. Unfortunately, the answer (i.e. optimal trait value, etc) may depend on which metric we choose. This is because that λ^{-a} term discounts the valueof offspring produced late in life. Intuitively, the the population is small and growing, a individual's proportional contribution to the gene pool is greater if offspring are produced now rather than later (when the population is larger).

Before we move on and make some simplifying assumptions, let's see what happens if we differentiate @(EL) with respect to some single parameter, say θ, on which fecundity and survival depend, in order to maximize fitness. Taking derivatives we have

(12)
$$0 = \sum_{a=1}^{\infty} -a\lambda^{-a-1}\frac{d\lambda}{d\theta}l_a\phi_a + \lambda^{-a}\frac{d[l_a\phi_a]}{d\theta}$$

At a maximum, $d\lambda/d\theta = 0$ so the first term drops out and we are left with

(13)

$$0 = \sum_{a=1}^{\infty} \lambda^{-a} \left[l_a \frac{d\phi_a}{d\theta} + \phi_a \frac{dl_a}{d\theta} \right]$$

Equation @(dEL) indicates that at the optimal value of θ any gains (losses) in fecundity that could be obtained by changing θ would be offset by losses (gains) in survival.

Why do things senesce?

Having a few measures of fitness in hand for age strucutred populations allows us to address some new questions. The first is why things senesce. The thinking here is less about optimality and more about evaluating how the strength of selection on vital rates changes with age. To measure the strength of selection, we will evaluate the change in fitness with respect to a change in age-specific survival or fecundty. Let's use R_0 as our fitness measure and see how this changes with a change in fecundity at some age, say a^*. Since $R_0 = \sum_{a=1}^{\infty} l_a \phi_a$, the derivative with respect to ϕ_{a^*} is

(14)

$$\frac{dR_0}{d\phi_{a^*}} = l_{a^*}$$

Evaluating the change with respect to age-specific survival, s_{a^*} is a little more complicated since these are buried inside the l_a terms. If $a \le a^*$ then $\frac{dl_a}{ds_{a^*}} = 0$. On the other hand, if $a^* < a$ then $\frac{dl_a}{ds_{a^*}} = l_a/s_{a^*}$. So the derivative of R_0 is then

(15)

$$\frac{dR_0}{ds_{a^*}} = \frac{1}{s_{a^*}} \sum_{a=a^*+1}^{\infty} l_a \phi_a$$

The foundational observation for understanding the evolution of senescence is that(14) and (15) are both decreasing functions of a^*. That is, the change in fitness for a change in either vital rate is greater early in life than later.

Age at maturation

The next question we will take a crack at is when to mature. Most organisms start out small andi spend some time growing prior to maturation. This delay in reproduction is profitable because larger individuals typically have higher fecundity and survival than smaller individuals of the same species. But how long should one wait? Intuitively, it only makes sense to delay maturation (and consequently risk dying before producing any offspring) if by doing so it is possible to increase the expected number of offspring you can produce in the future. And when we say 'in the future' this means all the way to the end. That is, if the expected lifetime reproductive output This could be accomplished either by increasing adult survival, increasing fecundity, or both.

To start, we'll let fecundity be some increasing function of the age of maturation, $\phi(A_m)$. Prior to age A_m fecundity is 0 and after maturation it is constant. One way to think about this is to imagine that fecundity depends on size and that growth is determinate in the organism we are considering. For simplcity, let's assume that the annual probability of survival is constant for adults and juveniles with values s_a and s_j respectively. So, for ages greater than or equal to A_m, the probability of surviving to that age is $l_a = s_j^{A_m} s_a^{a-A_m}$.

With these assumptions we can write the Euler-Lotka equation as

$$1 = \sum_{a=A_m}^{\infty} \lambda^{-a} s_j^{A_m} s_a^{a-A_m} \phi(A_m)$$

We can pull out the constant terms to simplify this a bit

(16)

$$1 = s_j^{A_m} \phi(A_m) \sum_{a=A_m}^{\infty} \lambda^{-a} s_a^{a-A_m}$$

Next we'll sum the series using the identity

(17)

$$\sum_{i=0}^{\infty} x^i = \frac{1}{1-x}$$

which is true provided that $|x|<1$. Applying this handy trick to (16) we get

$$1 = s_j^{A_m} \phi(A_m) \frac{1}{1 - s_a/\lambda} \lambda^{-A_m}$$

which we can re-arrange as

(18)

$$\lambda^{A_m} [1 - s_a/\lambda] = s_j^{A_m} \phi(A_m)$$

So far, all we've done is simplify the Euler-Lotka equation a bit, but at this point it is clear that we still arent going to end up with an explicit equation for for fitness. This polynomial is the best we are going to do. But we can still make some progress.

To find the age of maturation that maximizes fitness, we find where the derivative of λ with respect to A_m is equal to 0. Differentiating (18) is kind of big, so we'll do it in a few steps. The easiest piece is to differentiate the right hands side, which gives

(19)

$$s_j^{A_m} \phi(A_m) \ln s_j + s_j^{A_m} \frac{d\phi}{dA_m}$$

The next step is to differentiate λ^{A_m}. Doing so gives

(20)

$$\frac{d\lambda^{A_m}}{dA_m} = A_m \lambda^{A_m-1} \frac{d\lambda}{dA_m} + \lambda^{A_m} \ln \lambda$$

We can use this (and a bit of factoring) to find the derivative of the left hands side

(21)

$$\lambda^{A_m-1} \frac{d\lambda}{dA_m} [A_m + s_a/\lambda] + \lambda^{A_m} [1 - s_a/\lambda] \ln \lambda$$

Now, we set (21) and (19) equal to each other. But before we do, recall that we want to find the point where $\frac{d\lambda}{dA_m} = 0$, so let's do that at the same time to get

$$\lambda^{A_m} [1 - s_a/\lambda] \ln \lambda = s_j^{A_m} \left[\phi(A_m) \ln s_j + \frac{d\phi}{dA_m} \right]$$

We are almost there. The last thing to do is make use of (18) on the left hand side to get

$$s_j^{A_m} \phi(A_m) \ln \lambda = s_j^{A_m} \left[\phi(A_m) \ln s_j + \frac{d\phi}{dA_m} \right]$$

Now we can cancel a few things to arrive at the surprisingly simple

11

(22)

$$\ln \lambda = \left[\ln s_j + \frac{1}{\phi} \frac{d\phi}{dA_m} \right]$$

So, what does (22) tell us? A few things. The first is that in a stable population (i.e. $\ln \lambda = 0$), the optimal age at maturity would be where the percent gain in fecundity from waiting to mature is exactly balanced by juvenile mortality. The second thing this tells us is that the optimal age at maturation depends on the log of the growth rate of the population. For instance, if $\phi(A_m)$ is linear or decelerating, so that $\frac{1}{\phi} \frac{d\phi}{dA_m}$ decreases with age, the optimal age at maturity will be earlier in a growing population.

This is the end of what we got to in class. But there are certainly more things to do! Some of the more interesting questions to tackle are 1) how fast should a juvenile organism grow? and 2) why do things senesce?