

## 1 Why do some species only reproduce once?

High on the slopes of Mt. Kenya there are two species of giant lobelia. The plants are striking for their giant columnar inflorescences that dot the dry alpine hillsides. Upon closer inspection you notice that most of the plants are low growing rosettes, that can grow slowly for decades before finally producing their enormous flower stalks. Both species are quite similar in the general form and life history. However the two species have very different patterns of reproduction. One, *Lobelia telekii*, produces a single flowering stalk and the whole plant dies immediately after reproduction. It will grow for 40 to 70 years before reproducing in a single massive episode. The other, *Lobelia keniensis*, can produce several rosettes so, even though one rosette may die, the whole plant continues growing and reproduce many times over its life.

Given that the plants need decades to reach reproductive size, why should *Lobelia telekii* “give up” after a single bout of reproduction?

The strategy of reproducing only once is called “**semelparity**”.<sup>1</sup> The alternative strategy of repeated reproduction is called “**iteroparity**”. Both strategies are common. Semelparity is found in annual and biennial plants and many species of insects, as well as in some longer-lived organisms such as salmon.

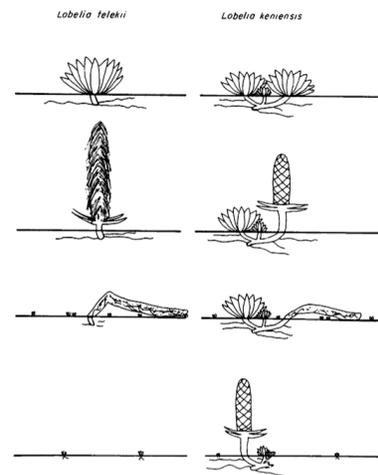
In *Lobelia*, as in all plants, the transition to flowering is an irreversible process. Once a particular meristem starts the flowering process, those tissues will differentiate into flowers and that branch will eventually die. *Lobelia telekii* is unbranched, producing a single rosette that eventually flowers and dies. *L. keniensis* branches belowground. Each flowering rosette will eventually die after flowering, but the side branches can continue growing to produce new rosettes that will continue the life of the individual.

The semelparous *Lobelia telekii* produces larger inflorescences than the iteroparous *L. keniensis*. Plants are able to translocate a certain amount of resources from one tissue type to another. Once flowering starts in *L. telekii*, a majority of the root biomass get resorbed and translocated to produce the massive inflorescences.

*Lobelia telekii* on Mt. Kenya



<http://dinets.travel.ru/mtkenya2.jpg>



from Young (1984)

<sup>1</sup> After Semele from Greek mythology, who died when she looked upon her lover Zeus after becoming pregnant only once.

Because *L. keniensis* continues to grow after flowering, the roots must be maintained. Fewer resources are available for reproduction and consequently the inflorescences are somewhat smaller.

In that way, the “decision” of when to reproduce has decisive consequences for the plant so it is reasonable to assume that the timing of that shift to reproduction has been under strong natural selection. Essentially, the decision is whether to commit all resources to flowering now, or to withhold some resources so the plant may be able to reproduce again sometime in the future.

### 1.1 What is the optimal strategy for reproduction?

One way to think about evolutionary strategies is to use an optimality argument. We know that fitness is maximized, so we can ask which phenotypes or strategies will produce the highest reproductive fitness. Optimality arguments have been very useful for understanding the costs and benefits of different strategies, but there are several assumptions that must be made in order to use optimality as a real model of evolution.

- ♦ Assumes that all phenotypes are possible. In fact the optimal phenotype may not be attainable because of constraints and tradeoffs.
- ♦ Assumes that there is sufficient genetic variation to produce all possible phenotypes.
- ♦ Ignores genetics. These models simplify the analysis by simply looking at the fitness of different phenotypes and we assume that phenotypes are inherited intact from parents to offspring. In essence, the two phenotypes are treated as if they were entirely separate asexual lineages that never interbreed or recombine to produce intermediate types.
- ♦ Assumes that other evolutionary forces (such as drift and migration) are unimportant.

On the other hand it may be reasonable to assume that, given enough evolutionary time, new mutations will continuously arise and those that confer higher fitness will eventually become fixed in the population. If natural selection is the dominant evolutionary force, we may expect populations to have phenotypes that are approximately optimal.

1.1.1 [Proceed by asking: “if there is a new mutation that changes life history by  $xx$ , will it spread in the population?”]

### 1.2 A thought experiment:

We’ll imagine a population that starts with two types of plants, semelparous and iteroparous. The type with the highest fitness will be expected to eventually dominate the population. To make things easy, we’ll assume that the population has reached the carrying capacity of the environment, so the total number of plants is fixed. One way to think about that situation is that there are a certain number of locations in the environment, each with enough resources for a single adult plant. To keep the population size constant, the only way a new individual can become established is if one of the adults dies, freeing up a site for a new plant.

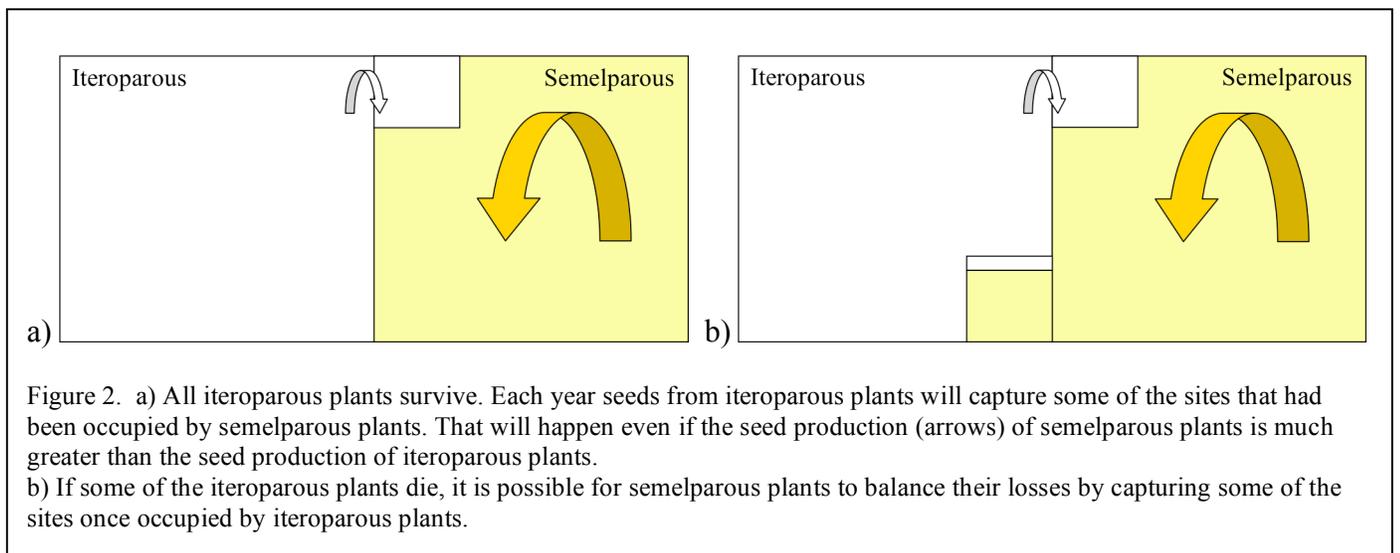
After each reproductive episode, the semelparous plants die and open up new sites for colonization, but the iteroparous plants produce a new rosette and continue growing. What happens to the numbers of semelparous and iteroparous plants over time?

Each generation the semelparous plants die and then those sites are colonized by a mix of seeds from the semelparous and iteroparous adults. Therefore only a fraction of the sites vacated by semelparous plants will be again colonized by semelparous types. Even if the number of semelparous seeds far outweighs the number of iteroparous seeds, the probability of that site being maintained by a semelparous type is less than 1.0, so the fraction of semelparous plants in the population will decline.

The number of iteroparous plants in the next generation will be all of the current iteroparous plants (which all survive) *plus* any seeds of iteroparous plants that are able to establish in the vacant sites. Therefore the fraction of iteroparous plants will increase each generation.

Truman Young has termed this the “poppy paradox”: how can semelparous strategies *ever* evolve? Nevertheless, we see many species that are semelparous.

To find the solution to this paradox we must go back and examine our assumptions in setting up the thought experiment. The flaw is that we assumed all of the iteroparous adults survive. If some of those adults also die, it is possible for the semelparous types to capture new sites that were once occupied by iteroparous plants and balance the losses of their own sites. If enough of the iteroparous adults die, it is possible for the semelparous plants to even increase and eventually become fixed in the population. That is especially likely if semelparous plants produce many more seeds than iteroparous plants, in which case vacant sites will be more likely colonized by a semelparous plant than an iteroparous plant.



### 1.3 How large must the fecundity advantage of semelparous plants be?

To determine how large the fecundity advantage of semelparous plants must be, we can formalize our thought experiment in an algebraic model.

Assume there is a population of Lobelias, with a mix of  $N_s$  semelparous and  $N_i$  iteroparous plants. The population is filled to carrying capacity, so we can imagine there are a fixed number of potential sites, each filled by a single plant. Because we assumed the population is at carrying capacity, a new plant can become established only when one of the existing adult plants dies.

Semelparous plants flower, produce  $b_s$  seeds, and then die. Iteroparous plants flower, produce  $b_i$  seeds, but also survive by producing another rosette. The mortality rate of iteroparous plants is  $m_i$ .

Each generation, all  $N_s$  sites occupied by semelparous plants become open, and a fraction ( $p_i$ ) of those sites become colonized by a seed from an iteroparous plant. The number of those sites that are lost is thus  $p_i N_s$ . At the same time, some of the sites occupied by iteroparous plants become open when iteroparous plants die ( $m_i N_i$ ) and a fraction ( $p_s$ ) of those sites are colonized by seeds from semelparous plants. The number of sites gained by semelparous plants is  $p_s (m_i N_i)$ .

At equilibrium, the number of sites lost to iteroparous plants must equal the number of sites gained from iteroparous plants

$$p_i N_s = p_s (m_i N_i) \quad \text{eq. 1}$$

The colonization probability is simply the fraction of seeds that are produced by a given type:

$$p_s = \frac{b_s N_s}{b_s N_s + b_i N_i} \quad \text{and} \quad p_i = \frac{b_i N_i}{b_s N_s + b_i N_i}.$$

Therefore equation (1) becomes:

$$\frac{b_i N_i}{(b_s N_s + b_i N_i)} N_s = \frac{b_s N_s}{(b_s N_s + b_i N_i)} (m_i N_i)$$

To simplify, we multiply both sides by the quantity  $(b_s N_s + b_i N_i)$  and divide both sides by  $N_i$  and  $N_s$  and rearrange to get:

$$\frac{b_s}{b_i} = \frac{1}{m_i} \quad \text{eq. 2}$$

If the mortality rate of iteroparous adults is very low, then the semelparous type must have a large fecundity advantage over the iteroparous type. As the mortality of the iteroparous type increases, the required fecundity advantage becomes less.

Equation 2 holds for any population that is not growing (i.e. at the carrying capacity). If  $\lambda$  is not equal to 1.0 then the derivation is slightly more complex but you end up with the same basic equation:

$$\frac{b_s}{b_i} = \frac{1}{1 - \frac{s_i}{\lambda}}$$

### 1.4 Data from Lobelias

The critical parameters to test this model are the survival of adult plants and the relative fecundities of semelparous and iteroparous plants. In these long-lived plants there is not much mortality, so it is difficult to measure survival accurately. But for this system the process is made easier because “plants stand still to be counted”! It is possible to mark plants and then return after months or years to see which ones are still alive.

Truman Young (1984, 1990) monitored several populations of these Lobelias for 8 years. He marked 1000 *L. telekii* plants and 1150 *L. keniensis* plants of various sizes with a small, numbered, aluminum tag. Every 6 weeks he visited the plants record mortality. Some of the plants wilted and died before reproduction, apparently from drought. Others were eaten by rock hyraxes, a rabbit-sized mammal that lives in the rocky slopes where *L. telekii* grows. Every three months he also measured the size of each plant by counting the number of leaves in the rosette and measuring the length of largest leaf.

The sample of *L. keniensis* plants included about 300 adult plants of reproductive size. In the wetter sites, only 9 of the 97 plants died during the 8 yrs of monitoring. That gives an average annual survival of  $\left(\frac{9}{97}\right)^{\frac{1}{8}} = 0.988$ . In the drier sites the mortality was slightly higher: 12 out of 98 plants died for an average annual survival of 0.984 and in the very driest sites annual survival was only 0.972.

Complete this table for survival in the dry sites.

Species	Habitat	Annual adult survival (s)	Years between reproductive episodes (t)	Cumulative survival between reproductive episodes (s <sup>t</sup> )	Required fecundity advantage for a switch to semelparity (1/(1-s <sup>t</sup> ))
<i>L. keniensis</i>	wet	0.988	7.2	0.917	12.0
	dry	0.984	13.9	0.799	5.0
	very dry	0.972	16		
<i>L. telekii</i>	very dry	(0.953)	(16)		

(*L. keniensis* data from Young 1990; *L. telekii* data from Young 1984)

Cumulative survival will be the *product* of survival each year between flowering episodes<sup>2</sup>. Therefore the cumulative survival after t yrs will be s<sup>t</sup>. In wet sites the average annual survival is

<sup>2</sup> from the product rule of combining probabilities, because the plant must survive this year AND next year AND the year after that, etc.

0.988, so the cumulative survival over 7.2 years between flowering episodes is  $0.988^7 = 0.917$ .<sup>3</sup>

Is iteroparity the optimal strategy for *L. keniensis* under these conditions? Using equation (2) we can ask what relative fecundity would be required for semelparous mutant to spread in this population. The cumulative mortality between reproductive episodes is 0.083, so the fecundity of the semelparous mutant would have to be more than 12 times higher than the iteroparous plants in order for it to have higher fitness.

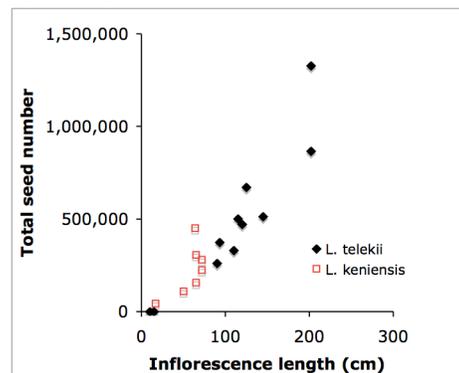
In dry sites the average annual survival of *L. keniensis* is lower (0.984) and the plants grow more slowly so the average time between flowering episodes is longer (13.9 yrs). In those habitats the cumulative survival between reproductive episodes is only 0.80, which corresponds to a cumulative mortality of 20%. Thus, in dry sites, a semelparous mutant would only need to produce 5x more seeds in order to spread in the population.

- ♦ *Lobelia telekii* occupies even drier habitats on the rocky slopes. All of the *L. telekii* plants died after reproducing, but we can approximate the adult survival rate by looking at the survival of large rosettes. Annual survival of large *L. telekii* rosettes in those habitats is even lower (0.953). If we assume 16 yrs between reproductive episodes of a hypothetical iteroparous plant in those habitats, what would the cumulative survival be? What is the required fecundity advantage of semelparous plants under those conditions?

### 1.5 What is the actual fecundity advantage of semelparous Lobelias?

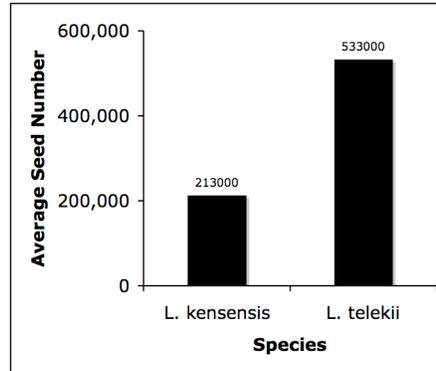
*Lobelia telekii* produces larger inflorescences than *L. keniensis* because it is able to translocate many of the resources from roots to reproductive structures.

Reproductive plants are relatively rare, so Truman Young sampled several additional populations from a range of different habitat types. Each flowering plant he measured the inflorescence height and rosette size at reproduction. Then on a subset of plants he estimated seed production. He counted the number of pods in each 10 cm segment inflorescence and counted seeds in 4 pods from each segment. It turns out that total seed production is a simple function of inflorescence height. Each species produces about 4000 seeds per cm of inflorescence.



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<sup>3</sup> You cannot combine mortality probabilities in the same way because each individual can only die once. It makes no sense for them to die this year AND die next year! Instead, calculate the cumulative mortality probability as  $1.0 - \text{cumulative survival}$ .



From those data, what is the proportional fecundity advantage for *L. telekii*?

### 1.6 Is iteroparity of *L. keniensis* still favored in ecologically marginal habitats?

Although *L. keniensis* is normally found on the valley bottoms instead of the dry slopes, some outlying populations do occur in sites that are much drier than normal. In those populations from very dry habitats the annual rosette survival of *L. keniensis* is only 0.972 and there are about 16 yrs between flowering episodes. Is iteroparity still favored in those very dry habitats?

What is the cumulative survival between reproductive episodes? How large of a fecundity advantage would there have to be in order for semelparous plants to have higher fitness than iteroparous plants? How does that compare to the actual fecundity advantage of *L. telekii*?

Simulations of populations of semelparous and iteroparous plants, as in figure ???. Black square are semelparous plants, white squares are iteroparous plants.

