Life History Strategies
Ethology and Behavioral Ecology

Introduction

Life history traits include factors such as:

- the number of offspring produced (or some stand-in such as the number of eggs produced[1]
- the timing of these offspring -- when are they produced over a female's life
- the survival of individuals from one time period to the next (and therefore, longevity).

All of these characteristics are heritable to some degree. Therefore, the life history traits of a population are subject to modification by natural selection. Moreover, notice that they are inter-related. Change in one type of life history trait could well involve trade-offs with another. For instance, having offpsring at an earlier age could easily affect (in this case decrease) surival of both the offspring and the parent.

Life history traits have many uses in biology. Population and conservation ecologists use them to make quantitative predictions about the future sizes of populations, future reproduction rates and the age distribution of members of the population. These estimates are not only important in understanding the role of a population within a given biological community but they are vital in designing management and recovery plans for economically important and endangered species.

On the other hand, for behavioral ecologists, life history traits are vital in the understanding of the "evolutionary decisions" an individual makes[2]. Life history traits can be fundamental to the understanding of behavior because many involve trade-offs of one behavior vs. another or trade-offs that lead to one behavior becoming better than another. For instance, in many species, the age of first reproduction, the reproductive period, and the life expectancy are very different in males and females. These differences in life history parameters are associated with significant differences in male and female behavior. As with many things in biology, behavior and life history strategy are intricately interwoven.

> **Note:** It is important that you understand that life history traits (like a particular longevity or clutch size) can be selected and are not simply the result of environment (adequate food, number of predators, etc.). If you do not know why the traits listed above should be heritable, please think about them, about the environment, and how selective forces might act on each of these traits.

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[1] How is this different from fitness?

[2] Let's remember that statements like "evolutionary decisions" are shorthands. When we say things like this, we are **not** implying a conscious decision nor are we necessarily even implying that a given individual has any choice. **We are saying that heritable alternative life history strategies exist in the population and selection will decide which ones work best.**

Some Terms[3]

- **Fecundity**: the **reproductive rate**; usually expressed as **the number of daughters produced by each female per time**. Usually fecundity is given for some particular time interval (for example, the reproductive rate of females for age 1 to 2 years).

- **Reproductive Value (RV)**: the **average influence of an individual of some age on the future size of the population**. The reproductive value changes in interesting and not always obvious ways over an individual's life and it also depends on a number of other features, such as the growth rate of the population. Much of this handout will be concerned with understanding the RV. We will see that the RV is typically given one of two ways -- either as:
    - the **absolute reproductive value is the number of offspring an individual is expected to have in its remaning lifetime**

--OR

    - **the relative reproductive value is the expected remaining reproduction normalized against the expected lifetime reproduction of an individual who was just born**. As in our earlier considerations of fitness, this relative value obviously is immediately useful in making general evolutionary comparisons.

- **Residual Reproductive Value (RRV)**: the number or relative number of **offspring expected in the future after the present breeding season**.

Why not count offspring to males? For one thing, we really only need to consider one sex if the sex ratio is 50:50 which it is in most species -- both parents are required to produce offspring. If the population is asexual, males don't matter. And finally, there is the paternity problem. In many species, there are simply not easy and inexpensive ways to determine who the father is! Finally, note that for obvious reasons males are generallly not limiting on population growth whereas the number of females is limiting. (Why?)

Understanding Reproductive Value

In this section, we will see how reproductive value is calculated. The goal is not for us to learn how to make the calculation, but instead to understand the parameters that affect RV. To keep this simple, let's use the "number of offspring" version of RV. RV can be calculated as:

1a. **Reproductive Value = "Present" Reproduction + Future Contribution**
or

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[3] For these definitions I follow the standard use of the terms, for instance as given in many ecology texts (examples: Ricklefs, R. *Ecology* Chiron Press (any edition) or Pianka, E. *Evolutionary Ecology* 4th Ed. Harper and Row

1b. **Reproductive Value = present reproductive value + RRV**

Know these equations. Notice that both versions of eq. 1 refer to the expected effect of a female on a population starting at a particular point in her life. This point could be anytime. Next, notice that we **arbitrarily divide her reproduction** into the **present** time (whatever we decide that time is) and the **future**.

Notice that in both cases we are talking about reproductive value, not reproduction *per se.* Keep this in mind -- as a short hand it is common to simply talk about present and future reproduction. These terms are accurate with any population that is stable. However, in populations that are increasing or decreasing, reproductive values are different than the simple sum or present and future reproduction (see discussion below).

Normally, the "present" will refer to the present breeding season or some subdivision of it in the case of seasonal breeders (example: temperate habitat birds) or to some arbitrary portion of time in the case continuous breeders (example: many species of mice, some primates). As you might well imagine, "choices" made about present reproduction can affect what will happen in the future. For instance, attempts to rear a large number of offspring could easily weaken an individual such that it did not succeed in reproducing the next season. Alternately, it may well be that now is better than later. We'll look at these choices or trade-offs in more detail shortly.

The Calculation of Reproductive Value

Before looking at trade offs let's take a side trip and see how **RV** calculated from **actuarial (life table) parameters** such as **survival** and **birth rates**.

NOTE: You will **not** need to actually make these calculations but it will be useful to at least understand how they are done. Understanding how RV is calculated will give you a deeper awareness of the concepts of present reproductive value and RRV. And, if you are new to the ideas of life history parameters and life tables, it will give you some idea why these measurements are so important to ecologists and evolutionary biologists.

Let's start with a general "word equation". Assume we divide a lifetime into a series of time intervals[4]. These could be years, months, breeding seasons, or whatever. Then, an animal's RV at any point of time in its life (*i.e.*, the remaining

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[4] We will assume that animals are using discrete breeding seasons. As a result, we will use discrete equations that deal with the sum of events over a set time interval and where we show summations using the Σ symbol. On the other hand, if we considered continuously breeding populations, we would sum over infinitesimally short times and use integration.

reproduction it expects) would be the <u>sum of the expected effect of reproduction on the population for each time period that remains</u> in an individual's life:

2. RV = Σ {(prob. living through that time)* (age specific. birth rate) * (pop growth factor)}

where the summation sign refers to adding the value within the brackets for each age group (i.e, for each time interval of a typical lifetime). The probablility of living from the start to the end of a particular time period is an easy concept to understand, as is the idea of the birth rate during that time. However, what is this population growth factor? Before going further, let's see what it means:

<u>Population Growth and the Value of Offspring</u>

If a population's size is changing, then the time when an individual has offspring has an effect on the number of descendants that individual will have at some arbitrary time far in the future.

Assume that **<u>all individuals within the study population have the same lifespan[5] and have the same number of offspring</u>**.

Let's see what happens when these individuals have their offspring at different times in their lives. Thus, for this consideration assume that the only way that inidivduals differ ***<u>is</u>* <u>WHEN</u> *<u>they have the offspring</u>*** -- that is, in their **<u>inter-generational times</u>**:

- offspring <u>relatively early</u> in one's life means a <u>short intergenerational time</u>
- offspring r<u>elatively late</u> translates to a <u>long inter-generational time</u>
- alternatively, one could have <u>offspring at any random time</u> which is the <u>equivalent (on the average) of an intermediate generational time</u>

<u>Example #1: In a population that is growing it is better to have young early</u>. A short intergenerational time means that one's offspring will also be reproducing at an early age. Since the population is growing, conditions must be good and that chance that newly borne individuals will survive and reproduce is high.

Let's look at a numerical example. Imagine a population that reproduces continuously, has a 1 year lifespan, and where sexual maturity is reached at 3 months. Each female produces 3 offspring. Let's compare the results for two females in this population -- one who breeds as soon as she is mature and immediately has all three offspring (<u>breeds early</u>) and the other who waits till near the end of ther life to have her three (<u>late breeder</u>). We will look at their effects on the population 1 year and 3 months hence (this is our "arbitrary future date"):

Time (months)	Early Breeder	Late Breeder
0	self	self
3 months	self + 3 offspring	self
6 months	self + 3 offspring +9 grandchildren	self
9 montths	self + 3 offspring +9 grandchildren+27 great grandchildren	
1 year	DIES **<u>but</u>** 3 offspring +9	dies but just before produces 3

[5] However, please note that the lifespan my well be different between populations. For instance, we will expect that the lifespan of an individual in an expanding population will be greater than in a contracting population.

	grandchildren+27 great grandchildren+81 great-great granchildren	offspring
1 year 3 months	9 grandchildren, 27 great grandchildren, 81 g-g-gc, 243 g-g-g-gc	3 offspring

Notice that <u>per lifetime everyone has 3 offspring</u> but the early breeder has 120X more descendants after 1 year than does the late breeder! She has a far greatrer effect on the future population and therefore by virtue of her early breeding has a far greater RV.
You may ask, why doesn't this work all the time? The reason is simple. In an expanding population, it does work (it is good to breed early) because the **<u>chance that offspring will survive is relatively great</u>**. There are plenty of resources, little competition and disease and the reason the pop. is expanding is in part that more young survive to reproduce. So the scheme above works exactly as laid out.

- However, **<u>in a contracting population</u>**, danger is high. Perhaps resources are limited. Regardless of the cause, many offspring <u>do</u> die before they reproduce. Lifespans may in general be shorter but remember that it is **<u>assumed that females still all have the same lifespans and same number of offspring</u>** (in this case, **less than 1 female per female**). As soon as offspring are produced, there is danger that they will die. But they are safe as unborn (remember -- *we are comparing mothers who have identical life spans and reproduction* -- the only way they differ is when they have their identical number of kids). So <u>a female who waits essentially protects her young</u>. On the other hand, the female who has her offspring early exposes them to danger. At the end of some time, the late breeders have lost fewer of their decendants and therefore, even though the entire population is decreasing, their proportional representation is increasing!
- If both of the above are true (and they are), then **<u>in a stable population</u>**, it cannot matter when young are born. Lines that use early births have the advantage of the shorter generation time and the effect outlined above. However, death rates of young are higher than in an expanding population and so whatever advantage is gained by early birth is lost to the higher death rate. On the other hand, the loss is not so great that late births have the advantage. The middle of the cycle is the best time to have offspring.

Armed with these insights, let's look at the equation used to calculate the relative RV (RRV)[6] for any arbitrary time interval:

3. $$RV = \frac{V_{x'}}{V_{0'}} = \frac{\lambda^{x'}}{l_{x'}} \sum_{x=x}^{\infty} \lambda^{x}\, l_x\, b_x \Delta x$$

Let's take this equation apart. Starting with extreme right of the equation, the chance of living through a certain age is l_x, the number of female offspring born to each femalein the breeding season at age **x** is ***b*$_x$**, and the term **Δx** simply refers to one unit of age. Thus, if the chance of living through age x is 0.5 and the birth rate at age x is 0.5 offspring per time, then l_x b_x, Δx **= 0.25 female offspring per female.** The term λ^x is something called the geometric growth

[6] Be sure you realize that RV is not necessarily the same thing as fitness (W). There are cases when the RV=W but in other cases it will not. It is useful as a stand-in related to fitness but it cannot always be thought of as the exact equivalent of fitness.

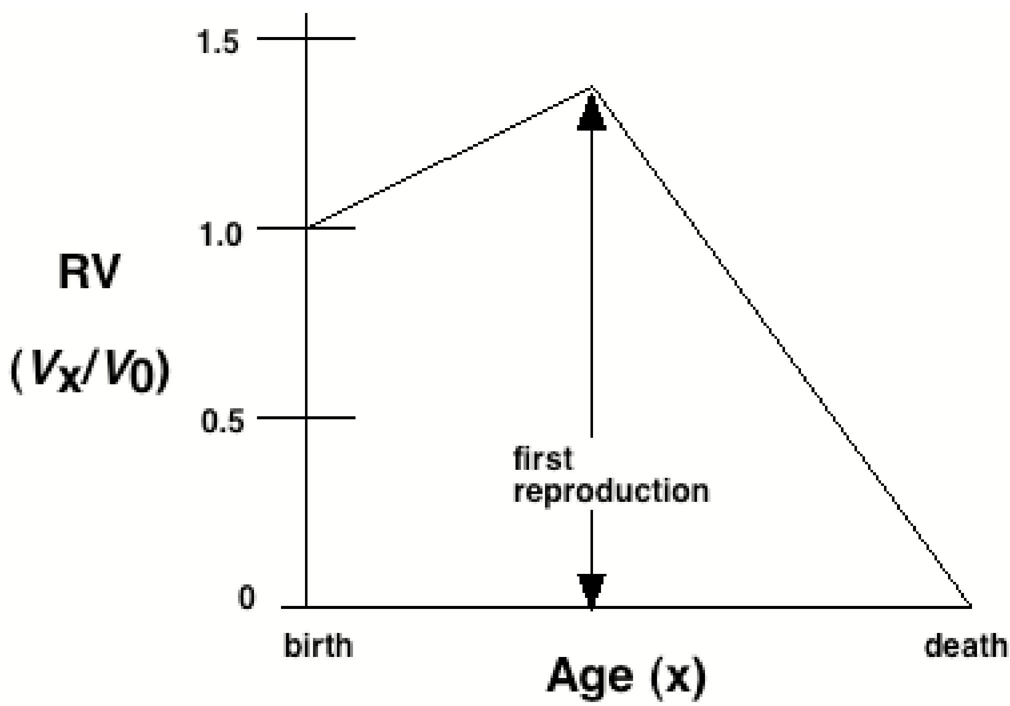
rate of the population. For instance, if the population is stable, λ is 1.0, if it is increasing $\lambda > 1.0$ and if the population is declining, $\mathbf{0 > \lambda < 1.0}$.

Notice the effect of λ is to discount or increase the effect of offspring at age x according to whether or not the population is growing (see box on preceeding pages). Thus, if the population is stable, λ is =1 and the product l_x b_x, Δ**x** remains as it is. If λ is >1.0, then the product is increased; if λ is < 1, it is decreased.

OK -- what about the (Σ) summation sign? The idea here is that we will **<u>sum</u>** the quantities $\lambda^x l_x$ b_x, Δ**x** for each time x interval that remains in the female's life (x to infinity) to get her present reproductive value (again, her influence as of now on the population size at some arbitrary time in the future).

We need not concern ourselves with the ratio $\frac{\lambda^{x'}}{l_{x'}}$, except to say that it also adjusts RV for population growth.

What does RV look like over a lifespan. The example below is typical and may surprise you (see next page):



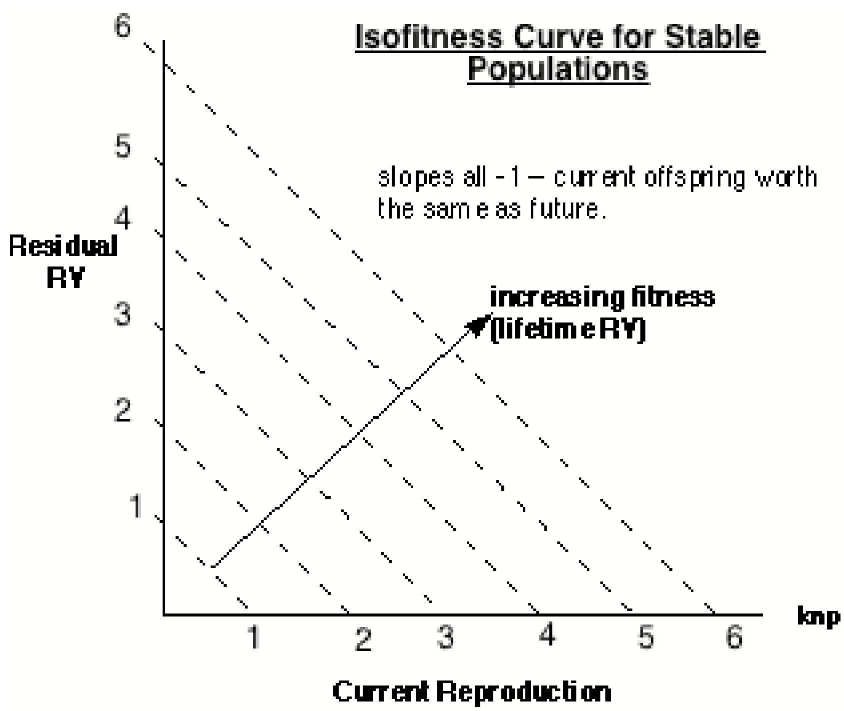
Notice that the RV is greatest at maturity (the age of first reproduction) -- not at birth. The reason should be evident after a moment of reflection. Let's assume that we are looking at the RV of a typical female. At birth, there is chance that she will not actually make it to sexual maturity. On the other hand, a sexually mature female has already passed this test and so the average number of lifetime offspring is greater tor the females that actually make it sexual maturity than the expected number per female at birth. As was stated on page 1, we often measure RV as a relative value and when we do we usually pick the RV at birth as the index for comparison. Thus, the graph shows RV initially as 1.0 followed by an increase to a maximum value when maturity is first reached. From there on, as the saying goes, it's all down hill!

<u>Visualizing LIfe History Decisions</u> --
<u>When and How Often to Reproduce in a Stable Population</u>

Now, let's use what we've learned to visualize some of the reproductive decisions that animals make. Recall from equation 1 that we can partition RV at any moment in an animal's life into present (this season) and future RV (residual RV -- RRV):

1. **Reproductive Value = Current Reproduction + RRV**

We can construct a graph of RRV vs present reproduction as a way of looking at these decisions: (next page)

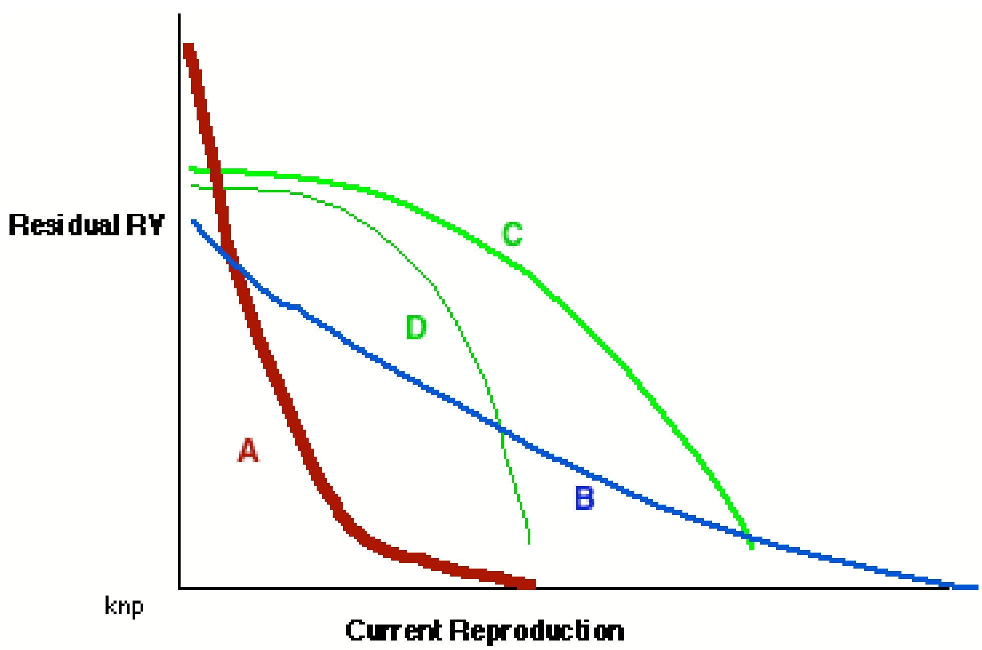


Notice that the graph features a series of lines connecting equal present reproductions and residual reproductions. Notice that every point on these lines (including the points on the RRV and F axes) has the same lifetime RV ("fitness"). Thus, these are curves of "**isofitness**" -- where fitness is everywhere the same.

The way to read an isofitness line is like this. Take the line with an isofitness value of "3". Here are some of the ways it can be achieved.

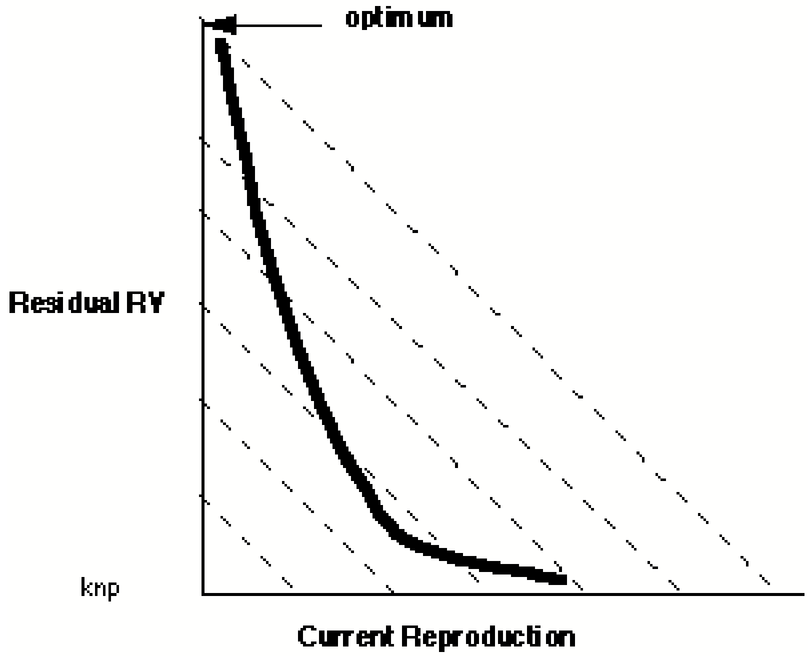
- All three offspring in the future (and therefore none now). Represented by point F=0, RRV=3).
- All three offspring now and none in the future (pt F=3, RRV = 0).
- Two now and one later (the point F2 and RRV1) -- notice it falls on the isofitness = 3 line. Thus, the line maps out all the possible ways to have three offspring such that lifetime W = RV = 3.

Now, let's suppose that for a given population or various individuals, you could measure or calculate the actual TRADEOFFS between present reproduction and RRV in terms of offspring. **If you know the population was neither expanding nor contracting**, you could plot the data on the isofitness space shown on the last page. Here are a number of such plots for different populations (but without the isofitness lines):



Each of these patterns actually occurs in nature. Moreover, several may occur in a given species. The shapes of the curves can be different for different aged individuals. Let's look at each curve and see what it means:

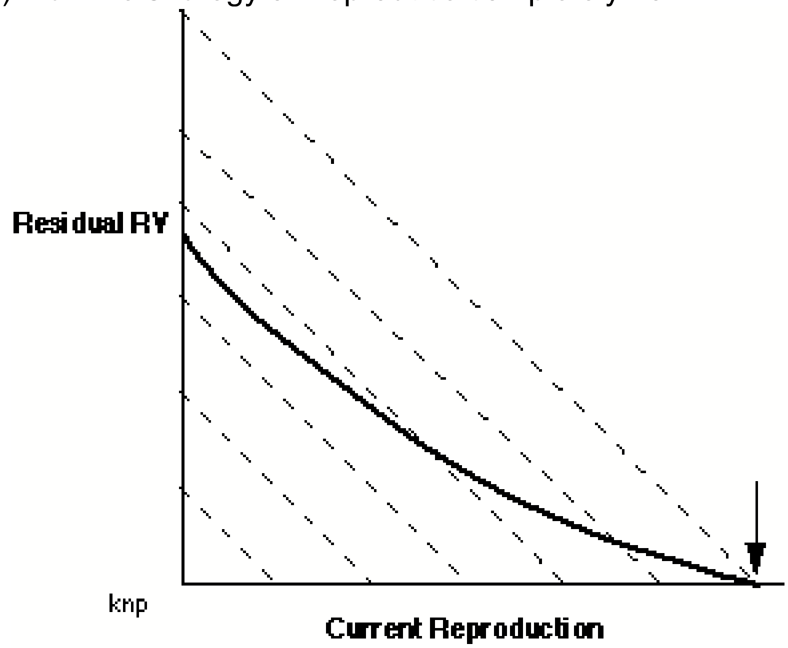
<u>Gambit #1 -- Delayed Reproduction</u>:



Notice in this population that the most successful strategy is to <u>delay reproduction</u>. If you calculate the RV for every point on the line -- that is, **<u>for each mix of present and future reproduction</u>**-- no point has a greater value (<u>combined present and future reproduction</u>) than the one given by having all reproduction in the future. Therefore, for this individual or population, that is the optimum.

Example: let's say that an organism has just reached sexual maturity but it is not fully grown. Further growth will mean it will tolerate reproduction better and produce more offspring. If there is a good chance it will survive, its curve will probably look like the one above and the best strategy is delayed reproduction.

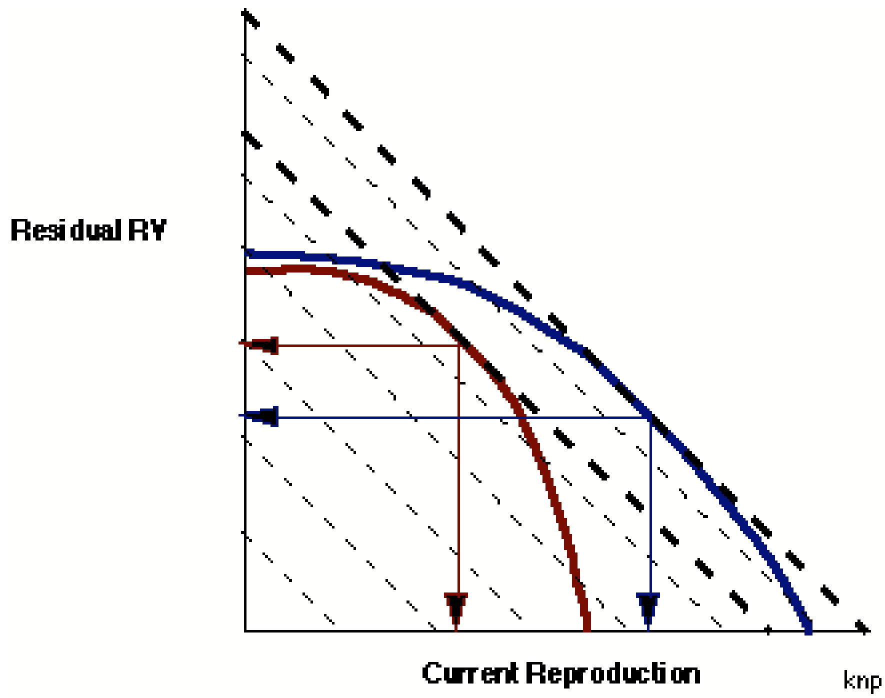
Gambit 2: <u>Semelparity</u> -- the "Big Bang"
Now, suppose instead that an organism is mature and able to reproduce but not likely to live till the next time period or, if it does live, it will have great difficulty reproducing. This is a very common reproductive strategy called **<u>semelparity</u>** where all reproduction is accomplished in one event or one short season. Notice this time that no point on the line has a higher fitness (present plus future reproduction) than the strategy of "reproduce completely now"!



These curves have the characteristic of being either **<u>concave</u>** (relative to the coordinate axes) or straight lines with the greatest value on the F axis.

<u>Final important note</u>: semelparity is especially **<u>common in situations where the initial costs of reproduction are high but once these have been met, the costs of additional eggs are very low</u>**. Think of animals that are semelparous and see if this principal is generally true.

<u>Gambit 3: Iteroparity</u>: In the final examples, notice that delayed reproduction and semelparity are <u>unable to beat a mixed strategy of some now and some later</u>. But of all the different versions of "some now, some later" one is clearly the best and therefore represents the optimum. This optimal strategy is the point where the <u>peak is tangent to the largest isofitness curve it touches</u>. Notice that these graphs are **<u>convex</u>**. This is shown on the top of the next page:



<u>Review Questions</u>

1. Be able to explain why graphs of semelparity and delayed reproduction are concave and iteroparity is convex.
2. Which of these curves best applies to salmon at sexual maturity? Explain.
3. Which overall best applies to a chickadee who has just become sexually mature? Explain.
4. Which best applies to humans at age 5? At age 25? Age 45? Explain.