A more general life history:

\[ F_x = \text{fecundity at age } x \]
\[ s_x = \text{survival from age } x \text{ to } x+1 \]

\[ \theta_x = \text{reproductive investment (fraction of resources devoted to reproduction) at age } x \]

Both \( F_x \) and \( s_x \) will be functions of \( \theta_x \) and all previous \( \theta \)s but not any subsequent \( \theta \)s.

That is, how much resource is put into reproduction at any given age will affect reproduction then and also will affect the resources available for survival and reproduction in the future, but cannot affect survival and reproduction at earlier ages.

If we could express fitness \( (\lambda) \) as an explicit function of the set of \( \theta \)s, we then could find the optimal \( \theta \)s by maximizing that function. This typically isn’t possible, though (remember that we can’t even get an explicit function for \( \lambda \) as a function of the \( s \) and \( F_s \)s).

Fortunately it can be shown — but won’t be — that the \( \theta_x \) that maximizes \( \lambda \) also maximizes the “reproductive value” at age \( x \).
Reproductive Value at age $x$, $V_x$:

The reproductive value of a female of age $x$ is her expected number of offspring from now (age $x$) until she dies except that the value of offspring born in the future is “discounted” relative to offspring born now.

In a growing population, early births contribute more to population growth because they begin reproducing sooner themselves than do later births. Another way to think of this is that at some time in the future the population will be larger than it is now, so that a single offspring is a smaller fraction of the total then than is a single offspring now.

Specifically, if the population is growing with finite rate of increase $\lambda$, it will be larger $w$ time steps in the future by a factor of $\lambda^w$, i.e. $N_{x+w} = \lambda^w N_x$. Thus a single birth at time $x$ will be $1/N_x$ of the population, while a single birth at time $(x+w)$ will be $1/N_{x+w} = 1/(\lambda^w N_x)$ of the population. The birth at time $(x+w)$ thus is worth $1/\lambda^w = \lambda^{-w}$ as much as a birth at time $x$.

Note that if the population is decreasing, $\lambda$ is less than 1 and a later birth is worth more than a birth now: if will be a larger fraction of the then smaller population.

Incorporating this discounting of future reproduction,

$$V_x = \sum_{t = x}^{\infty} \left[ (\text{survival from age } x \text{ to age } t) \cdot \lambda^{-(t-x)} \cdot b_t \right]$$

Survival from age $x$ to age $t = l_t / l_x$ and the $1/l_x$ term can be moved outside the summation.

$\lambda^{-(t-x)} = \lambda^{-t} \lambda^x$ and the $\lambda^x$ term also can be moved outside the summation.

So

$$V_x = \frac{\lambda^x}{l_x} \sum_{t = x}^{\infty} [l_t \cdot \lambda^{-t} \cdot b_t]$$

$V_x$ is scaled relative to the reproductive value of a newborn female, so $V_0 = 1$. 
$V_x$ also can be defined as

- the contribution of females of age $x$ to the population growth rate, or
- the total births now to females of age $x$ and older;
  in this case the $\lambda^{-(t-x)}$ "discounting" results from the population having been proportionally smaller by that factor — so that births were proportionally fewer — back when the females now age $t$ were born compared to when the females now age $x$ were born.

If the population is being counted just before the birth pulse (so the Leslie matrix would use fecundities, $F_x$, rather than births, $b_x$), the formula is slightly different:

$$V_x = \frac{\lambda x}{l_x} \sum_{t = x}^{\infty} [l_t \cdot \lambda^{-(t + 1)} \cdot F_t]$$

If reproduction is continuous rather than in pulses, the formula is analogous but uses the instantaneous rate of increase rather than the finite rate, and an integral rather than a summation:

$$V_x = \frac{e^{rx}}{l(x)} \int_x^{\infty} e^{-rt} \cdot l(t) \cdot m(t) \, dt$$

$V_x$:

- increases from birth until reproduction starts (because the probability of surviving to reproduce increases)
- typically peaks early in the reproductive period (because younger females have a longer remaining reproductive life than do older females)
Examples:

voles (*Microtus agrestis*)
in laboratory conditions

**Figure 8.2**
Curves of reproductive values for human populations in three countries (from Keyfitz 1985).

**Figure 8.3**
Reproductive values of rice weevils (from data in Birch 1948).
Reproductive value and life-history evolution:

As will be seen in the section of the course on population genetics, natural selection in many cases acts to maximize $\lambda$: if genotype fitnesses are density- and frequency-independent, the genotype with the largest $\lambda$ will increase fastest and become relatively more frequent.

Since reproductive value measures the contribution of females of a given age to $\lambda$, genetic variation affecting ages with high reproductive value will have greater effects on fitness than will variation affecting other ages. Thus selection tends to be strongest on traits expressed at ages of the greatest reproductive value.

Thus: aging, menopause, genetic diseases affecting the elderly, etc.
Returning to the optimization of age-specific reproductive effort, as noted earlier the \( \theta \) which maximizes \( V_x \) also maximizes \( \lambda \) and thus is optimal.

\( V_x \) can be split into two parts: \textbf{current reproduction} + \textbf{future reproductive value}:

\[
V_x = \frac{\lambda^x}{l_x} \sum_{t = x}^{\infty} [l_t \cdot \lambda^{-t} \cdot b_t]
\]

\[
= \frac{\lambda^x}{l_x} \left\{ l_x \lambda^{-x} b_x + \sum_{t = x + 1}^{\infty} [l_t \lambda^{-t} b_t] \right\}
\]

\[
= b_x + \frac{\lambda^x}{l_x} \sum_{t = x + 1}^{\infty} [l_t \lambda^{-t} b_t]
\]

\[
= b_x + \left( \frac{\lambda^x + 1 / \lambda}{l_x + 1 / s_x} \right) \sum_{t = x + 1}^{\infty} [l_t \lambda^{-t} b_t]
\]

\[
= b_x + \frac{s_x}{\lambda} \cdot \lambda^{x + 1} \sum_{t = x + 1}^{\infty} [l_t \lambda^{-t} b_t]
\]

\[
= b_x + \frac{s_x}{\lambda} \cdot V_{x + 1}
\]

Using the alternative form of \( V_x \) based on fecundities \( (F_x) \) rather than births \( (b_x) \), this separation of current reproduction and future reproductive value yields:

\[
V_x = \frac{1}{\lambda} (F_x + s_x V_x + 1)
\]

The second term, the product of the probability of surviving to the next age class times the reproductive value at that age (and divided by \( \lambda \) in the first formulation) is termed the “\textbf{residual reproductive value}.”
Notice that these expressions for reproductive value as the sum of current reproduction and residual (i.e. future) reproductive value,

\[ V_x = b_x + \frac{s_x}{\lambda} \cdot V_{x+1} \]

and

\[ V_x = \frac{1}{\lambda} (F_x + s_x V_{x+1}) \]

have essentially the same structure as the expression for \( \lambda \) in the simple life cycle considered earlier, which was

\[ \lambda = F + s_a \]

The difference is that with the more complex life cycle, the contribution of survival to the next age is proportional to the reproductive value of that next age. This produces the additional difference that life history strategies — \( \theta \) — at future ages can affect the optimal strategy at the focal age \( x \), since they affect \( V_{x+1} \).

The iterative form of the expression above for \( V_x \), as a simple function of \( V_{x+1} \), however, also shows that the optimal set of \( \theta \)s can be determined iteratively, starting with the oldest age class. For that age class, there is no later \( \theta \) to worry about. Once \( \theta \) is optimized for that age class, that determines its reproductive value, so the optimal \( \theta \) for the next oldest age can be determined, and so on.

At any given age \( x \), therefore, with \( V_{x+1} \) determined by optimizing the \( \theta \)s for all later ages, optimization of \( \theta_x \) is exactly analogous to the procedure for the simple life cycle considered before:

- \( b_x \) and \( s_x V_{x+1} \) are expressed as functions of \( \theta_x \), and
- the value of \( \theta_x \) which maximizes \( b_x + s_x V_{x+1}/\lambda \) is found.

Graphically this maximization is just like before for the simple life cycle, but with \( b_x \) and \( s_x V_{x+1}/\lambda \), or \( F_x \) and \( s_x V_{x+1} \), and their sum, plotted against \( \theta \).

Factors which reduce either the probability of surviving to the next age (\( s_x \)) or the reproductive value of that next age (\( V_{x+1} \)), will favor greater investment in reproduction, i.e. larger \( \theta_x \).

Factors which reduce the birth rate (\( b_x \)) attained by a given reproductive effort will tend to favor reduced reproductive effort.