Lack clutch size: maximize offspring per reproductive event

![Graph showing survival and yield vs eggs]

- **Survival**
  - Survival increases with clutch size up to 5 eggs, then decreases.
  - Max survival occurs around 5 eggs.

- **Yield (eggs x survival)**
  - Yield increases with clutch size up to 5 eggs, then decreases.
  - Max yield occurs around 5 eggs.

The graphs illustrate the trade-off between survival and yield, with optimal clutch size around 5 eggs for maximizing offspring per reproductive event.
Lack clutch size: maximize offspring per reproductive event

 Yield: (eggs x survival)

 Surplus: (1 - survival)
observed clutch sizes: smaller than Lack optimum
A tradeoff: adult survival also depends on reproductive effort (e.g. clutch size):

13 species of lizards (from Tinkle 1969, in Futuyma 1986)
optimal reproductive effort when **adult survival decreases** (and total fecundity increases) **with increasing reproductive effort**: 

simple life history:\n
\[
\begin{align*}
N_{t+1} &= (s_0B + s_a)N_t \\
\lambda &= s_0B + s_a = F + s_a \\
\end{align*}
\]

Optimal reproductive effort will maximize \( \lambda \).

Let \( \theta \) be the fraction of available resources devoted to reproduction (at each time step). Fecundity (\( F \)) will increase, and survival (\( s \)) will decrease, as \( \theta \) increases. For example:

\[
\begin{align*}
F(\theta) &= b \theta^c \\
s_a(\theta) &= a(1-\theta^d) \\
\lambda &= b \theta^c + a(1-\theta^d) \\
\end{align*}
\]

To maximize \( \lambda \), take its derivative and set equal to 0:

\[
\frac{d\lambda}{d\theta} = cb\theta^{c-1} - da\theta^{d-1}
\]

\[
\frac{d\lambda}{d\theta} = 0 \quad \text{when}
\]

\[
\begin{align*}
theta^{c-1}\theta^{d-1} &= da/cb \\
\theta^{c-d} &= da/cb \\
\theta_{opt} &= (da/cb)^{1/(c-d)}
\end{align*}
\]

in text (Box 7.2), \( c = 1/2, d = 2 \), so

\[
\hat{\theta} = \left( \frac{2a}{b/2} \right)^{-3/2} = \left( \frac{4a}{b} \right)^{-2/3} = \left( \frac{b}{4a} \right)^{2/3}
\]
So long as $c < 1$ and $d > 1$,
- the $F$ and $s_a$ curves will be convex and
- the optimal $\theta$ will increase with increasing ratio $b/a$,
  i.e. as fecundity increases relative to adult survival.

Remember that $F = bs_0$, so increasing either the birth rate or juvenile survival will increase the
optimal reproductive effort (all else remaining equal).

If $c > 1$ and $d < 1$,
- the $F$ and $s_a$ curves will be *concave* and
- the optimal $\theta$ will be either
  - 1 (semelparity) if $b > a$ (i.e. max $F > \max s_a$), or
  - 0 (never reproduce) if $b < a$

Why would the curves be *concave*?
  - yuccas & agaves (Shaffer 1974): strong competition for pollinators is associated with concave
    curve for $F$, and semelparity

How does the degree of convexity affect the optimal $\theta$?

When is semelparity optimal even with convex curves?
  - When $F$ is increasing faster than $s_a$ is decreasing even as $\theta$ approaches 1
**fitness set analysis** (Levins):

Since \( F \) and \( s_a \) both are functions only of \( \theta \), either one can be expressed as a function of the other, e.g.

\[
F = b \theta^c \quad s_a = a(1-\theta^d)
\]

Rearrange 2nd eqn. to express \( \theta \) in terms of \( s_a \):

\[
\theta = (1-s_a/a)^{1/d}
\]

Insert this into 1st eqn.:

\[
F = b (1-s_a/a)^{c/d}
\]

This curve represents the combinations of \( F \) and \( s_a \) produced by all values of \( \theta \) from 0 to 1.

We want to find the point on this curve which produces the maximum \( \lambda \). We can rearrange \( \lambda = F + s_a \) to again express \( F \) as a function of \( s_a \), i.e.

\[
F = \lambda - s_a
\]

This is a straight line with slope -1 and Y intercept = \( \lambda \); all points along such a line have equal fitness (\( \lambda \)).

The optimal strategy will be the point where the curve of \((s_a, F)\) just touches the highest straight line with slope -1.

**Comments** on the fitness-set method:

(1) Where the curve and the straight line just touch, the slope of the curve must be -1 (and it is shallower to the left and steeper to the right). So we could find the optimum analytically by taking the derivative of the \( F \) vs. \( s_a \) curve, setting it equal to -1, and solving for \( s_a \).

(2) The set of phenotypes could be expressed in terms of \( B \) and \( s_a \) (assuming \( s_0 \) is independent of reproductive effort). Then \( \lambda = s_0 B + s_a \) would be rearranged to give

\[
B = (\lambda - s_a)/s_0 = (\lambda/s_0) - (1/s_0)s_a
\]

So now in a plot of \( B \) vs. \( s_a \), equal-fitness contours are straight lines with slope of \(-(1/s_0)\).
Other life history tradeoffs:

- offspring number vs. offspring size
- parental care (increasing \( s_0 \)) vs. additional offspring
  *e.g.* altricial vs. precocial offspring
- timing of metamorphosis, migration, etc.
- dispersing vs. staying home
  (fitness consequences of dispersal typically depend on whether others are dispersing, so *game theory* rather than simple optimization may be needed)
- daughters vs. sons (i.e. sex ratio)
  (fitness consequences definitely depend on sex ratios produced by others, so *game theory* is needed)
- ??? others ???