LIFE HISTORY THEORY NOTES

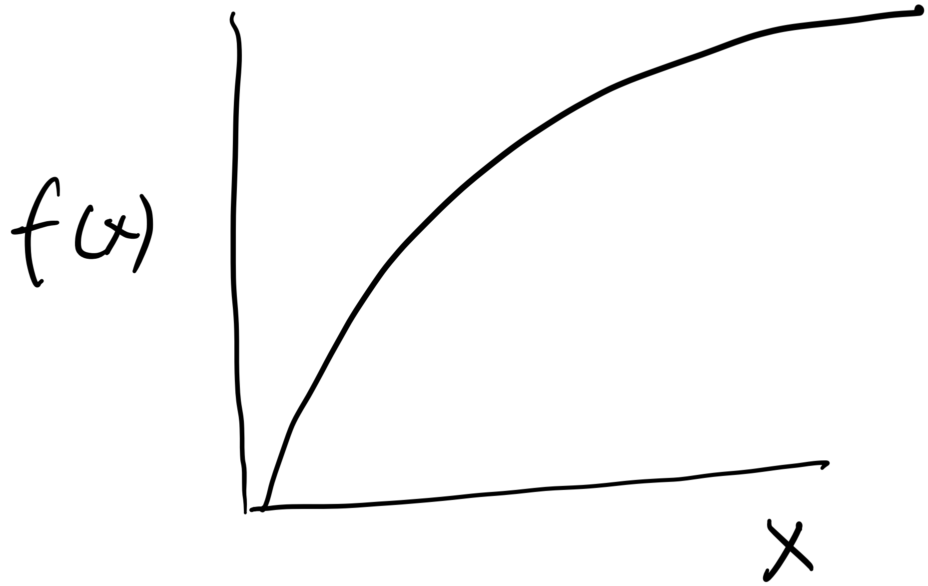
JAMES HOLLAND JONES

FALL 2020

Risk Lecture

Fitness/Utility Function
- nonlinear in input (energy, effort)
- increasing, concave

$$f'(x) > 0, \quad f''(x) < 0$$



- offspring produced later in life enter a larger population ⇒ lower marginal increase

Taylor series expansion of $f(x)$ around mean of x, $\bar{x}$:

$$f(x) = f(\bar{x}) + f'(x)(x-\bar{x}) + \frac{1}{2} f''(x)(x-\bar{x})^2 + \dots$$

Take Expectations of both sides:

$$\overline{f(x)} = f(\bar{x}) + \frac{1}{2} f''(x) \, Var(x)$$

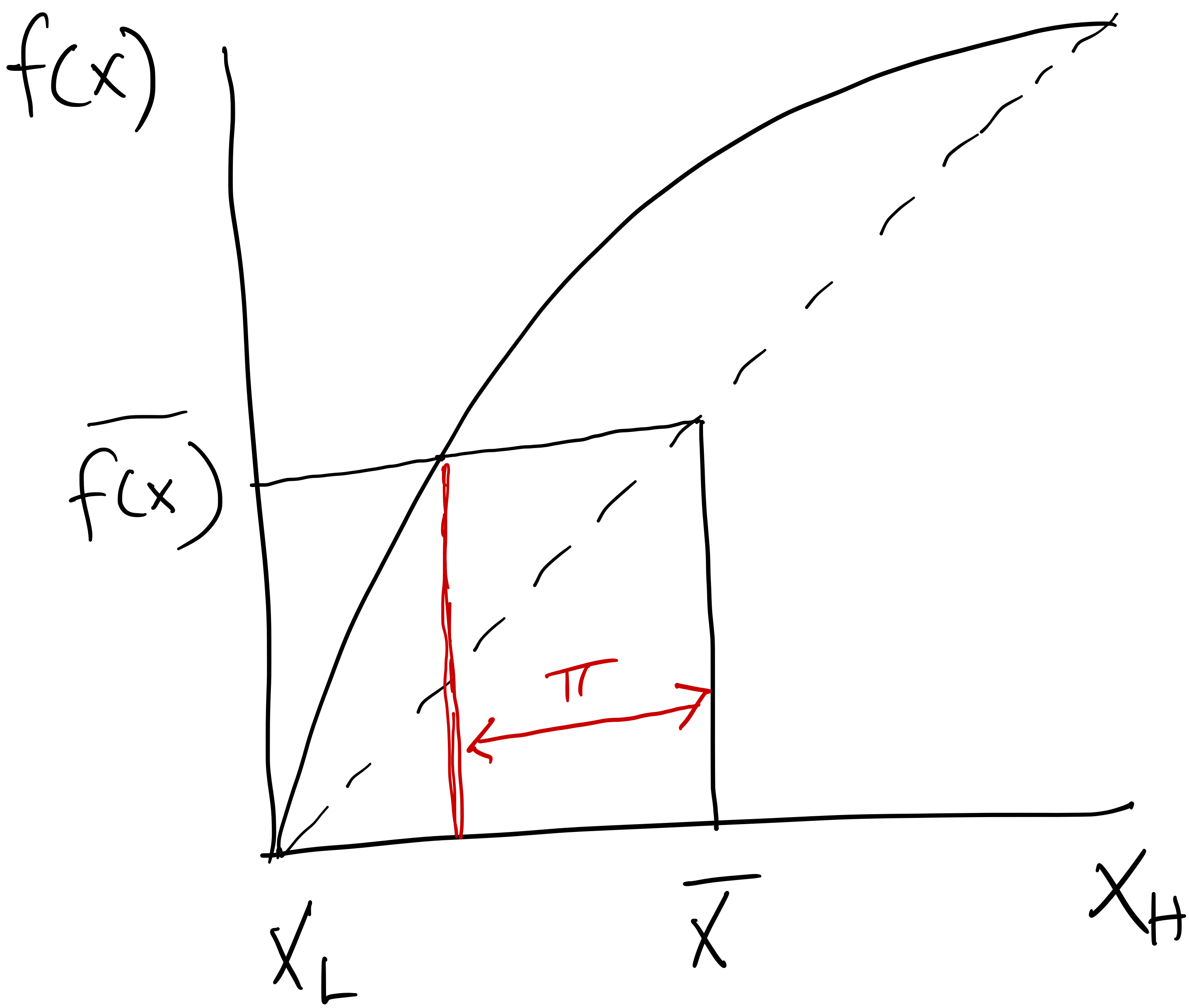
$$\mathbb{E}(x-\bar{x}) = 0$$
$$\mathbb{E}(x-\bar{x})^2 = Var(x)$$
$$\mathbb{E} f(\bar{x}) = f(\bar{x})$$

$$f(x) = f(\bar{x}) + \frac{1}{2} f''(x) \mathrm{Var}(x)$$

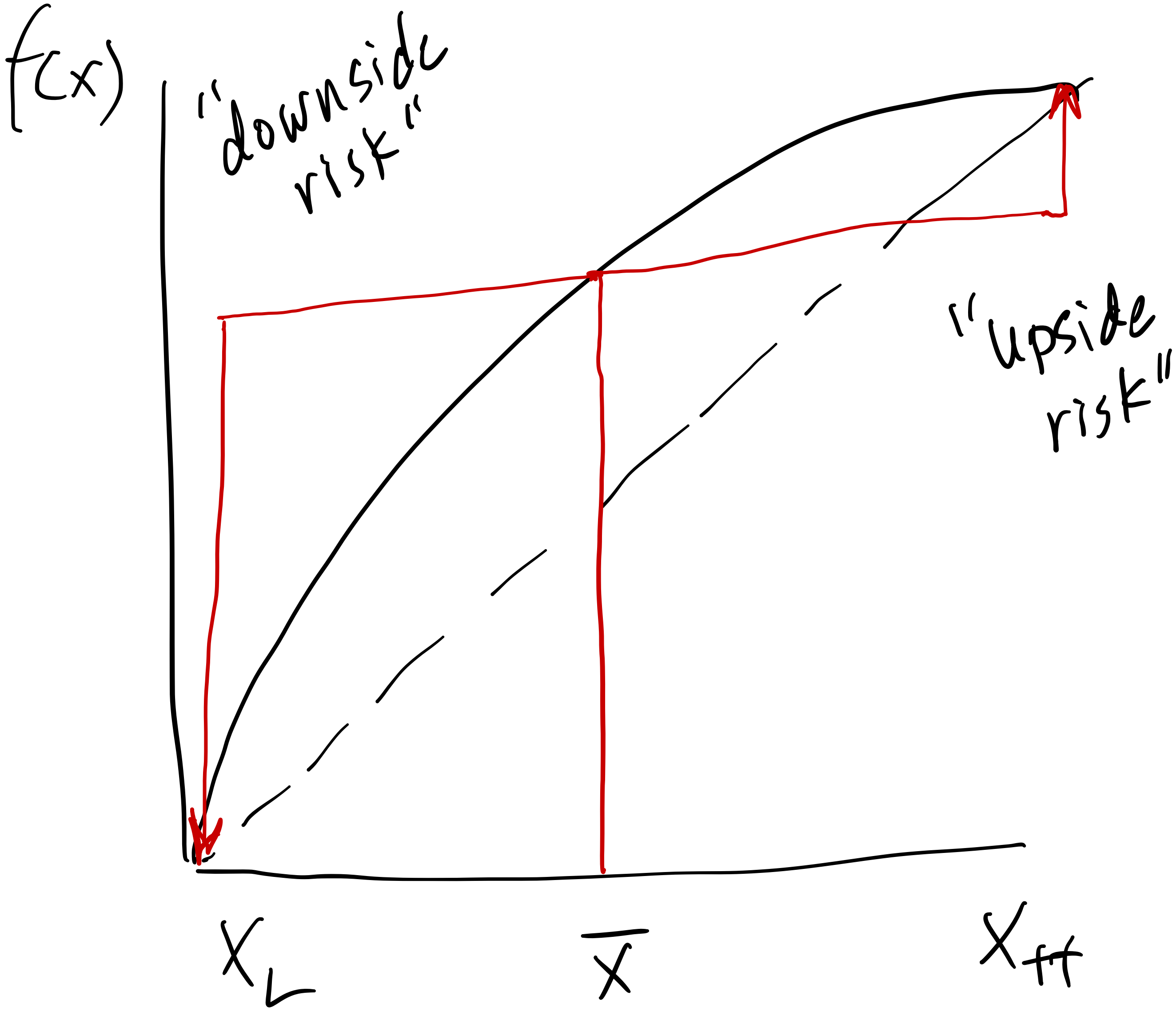
- fitness function, $f(x)$, has negative 2^{nd} derivative by assumption (and generally biological reality)

- shows that variance is generally bad for fitness since $\frac{1}{2} f''(\bar{x}) \mathrm{Var}(x) < 0$

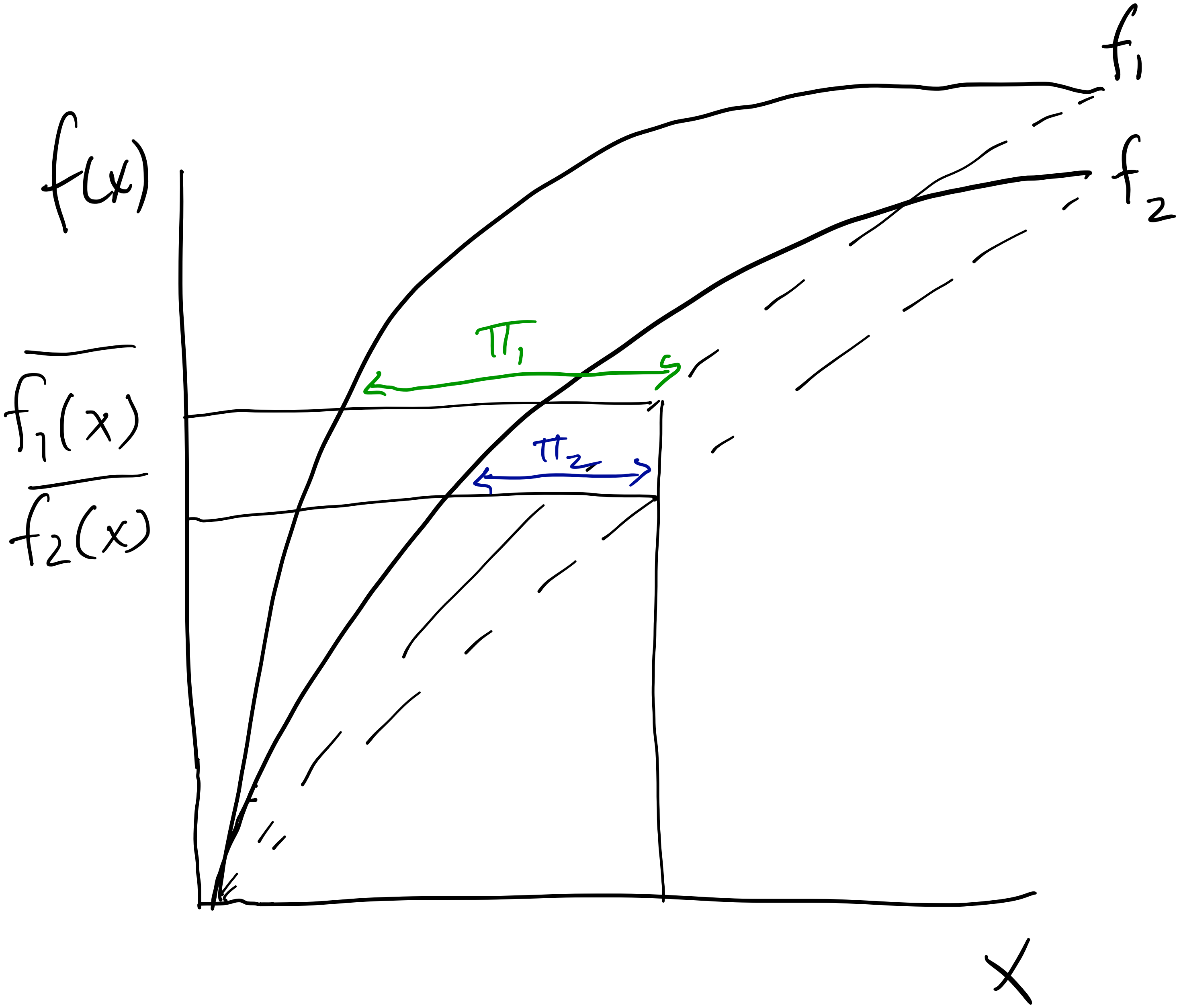
Risk-Aversion + Certainty Premium



- Since $f(\bar{x})$ lies below $f(x)$, draw a line back to $f(x)$ curve. That point has equivalent fitness.
- difference between these 2 x points called <u>certainty premium</u>, π. It's the amount a risk-averse agent should be willing to pay for certainty



Curvature of f(x) creates a substantial asymmetry between downside-vs.-upside risk!



$$A_u = \frac{-f''(x)}{f'(x)}$$

$$\mathbb{E}\left[u(x+\epsilon)\right] = u(x-\pi)$$

$$\mathbb{E}\left[u(x) + \epsilon u'(x) + \frac{\epsilon^2}{2} u''(x)\right] =$$

$$u(x) - \pi u'(x)$$

Note: $\mathbb{E}(\epsilon) = 0$

$\mathbb{E}(\epsilon^2) = \sigma^2$

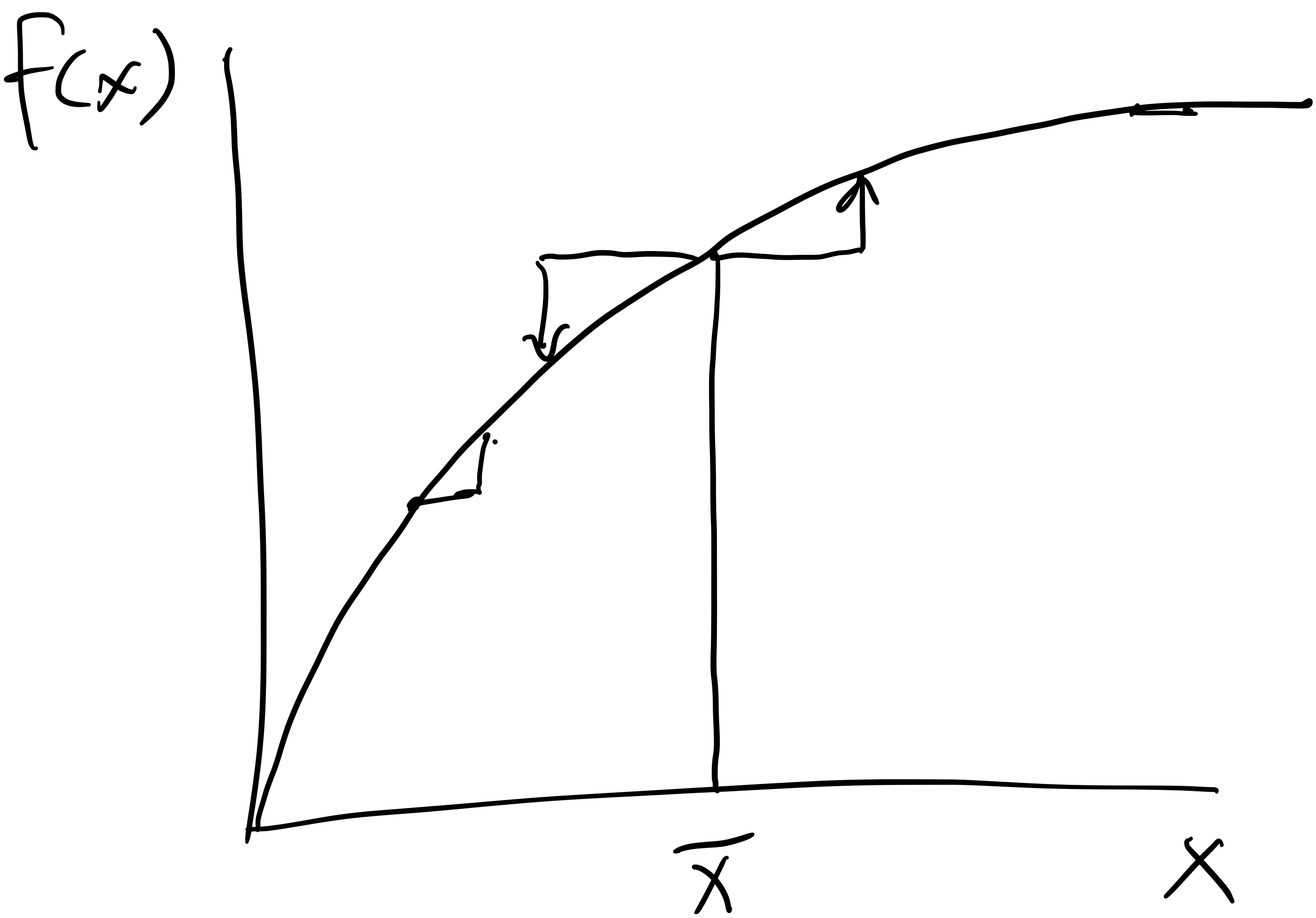
$$-\frac{u''(x)}{u'(x)} = A_u$$

$$\boxed{\pi \approx \frac{\sigma^2 A_u}{2}}$$

Fitness : $f(x)$

- nonlinear input
- increasing, concave

$f'(x) > 0$, $f''(x) < 0$



$$f(x) = f(\bar{x}) + \underline{\underline{f'(x)(x-\bar{x})}}$$

$$+ \frac{1}{2} f''(x) \underline{\underline{(x-\bar{x})^2}} + \dots$$

$$\overline{f(x)} = f(\bar{x}) + \frac{1}{2} f''(x) \mathrm{Var}(x)$$

$$\mathbb{E}(x-\bar{x}) = 0$$

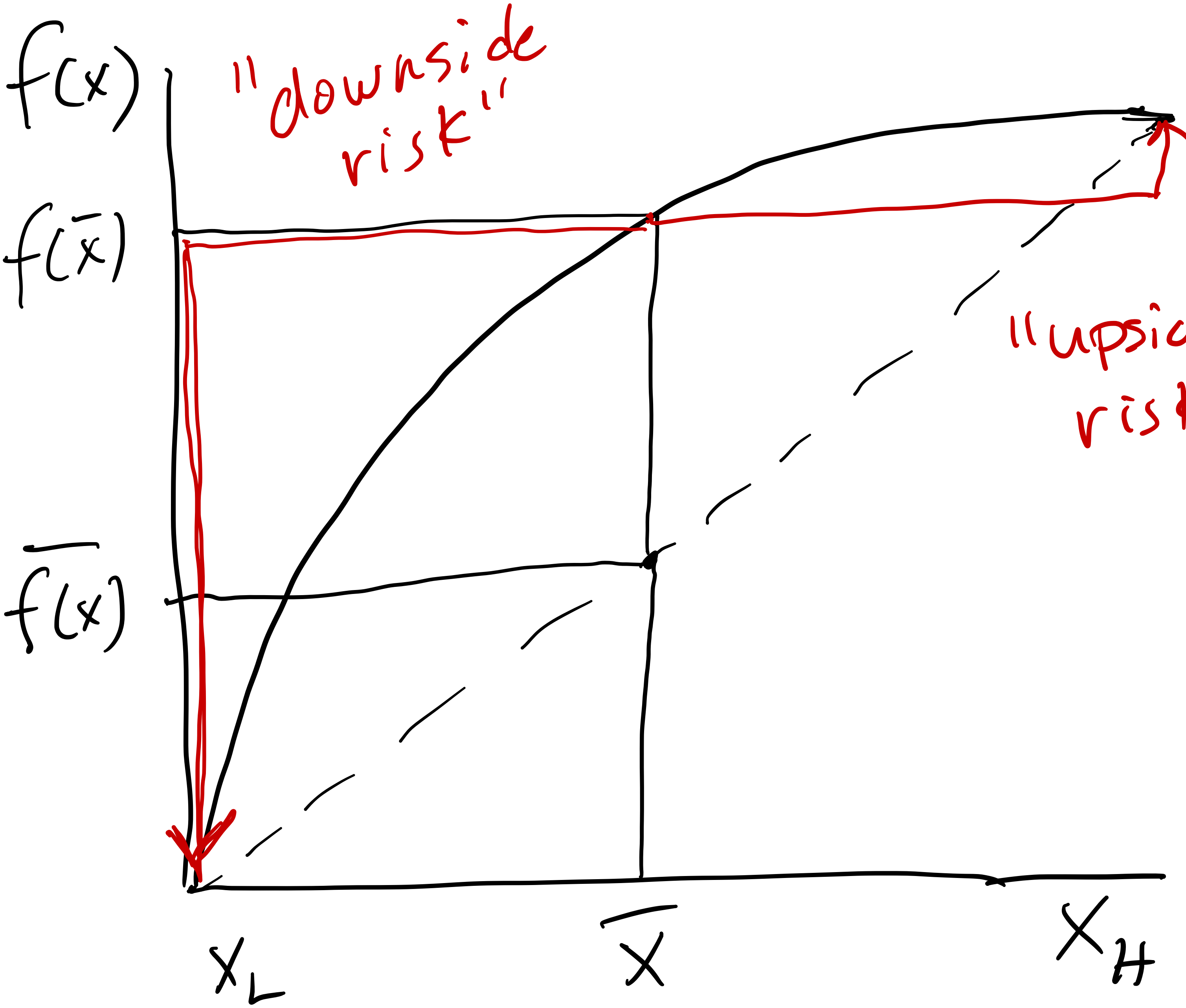
$$\mathbb{E}(x-\bar{x})^2 = \mathrm{Var}(x)$$

$$\mathbb{E}(f(\bar{x})) = f(\bar{x})$$

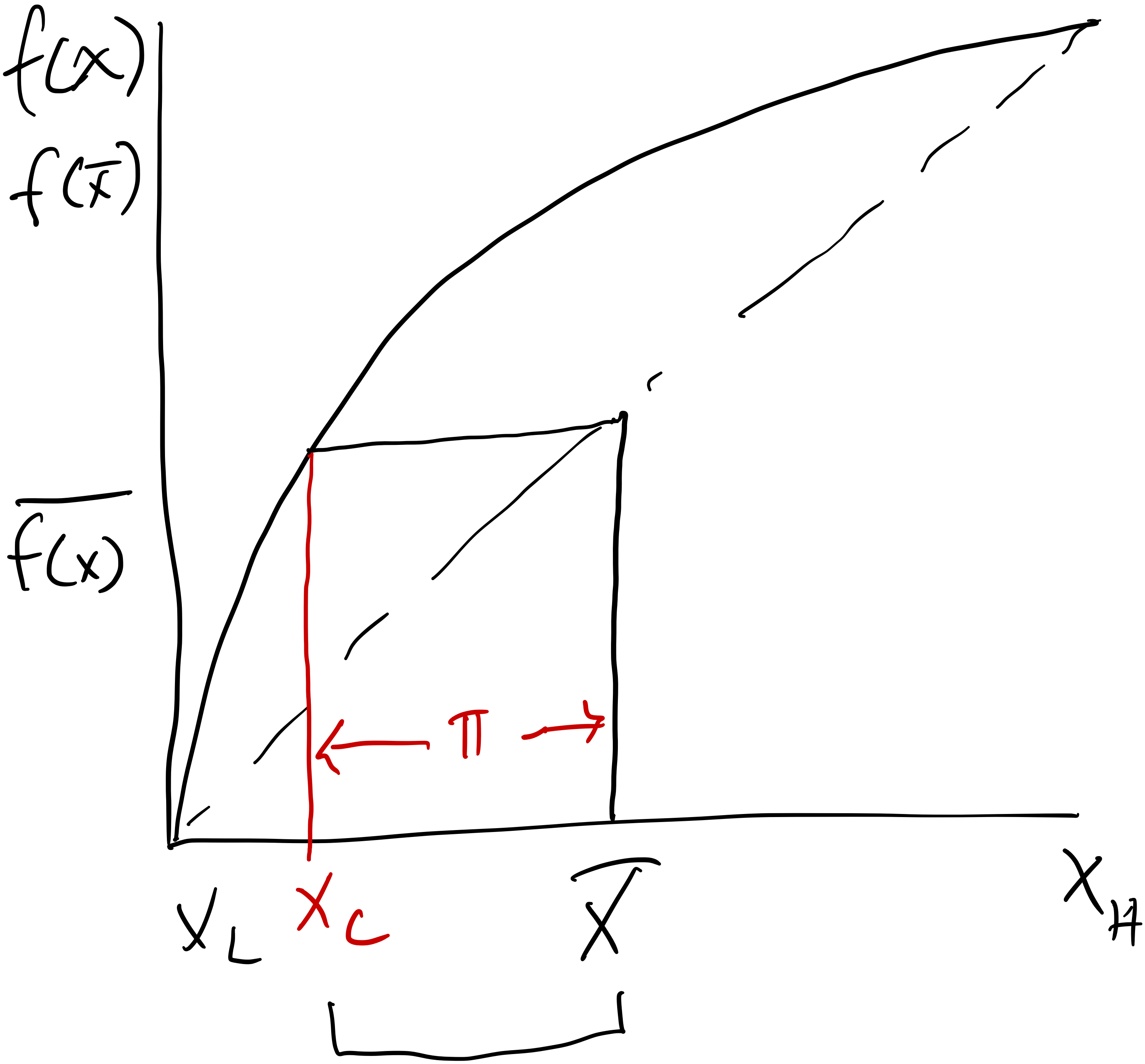
$$f(x) \approx \underline{f(\bar{x})} + \underline{\frac{1}{2} f''(x)} \underline{Var(x)}$$

- fitness function, $f(x)$, has negative 2^{nd} derivative by assumption (and by biological realism)

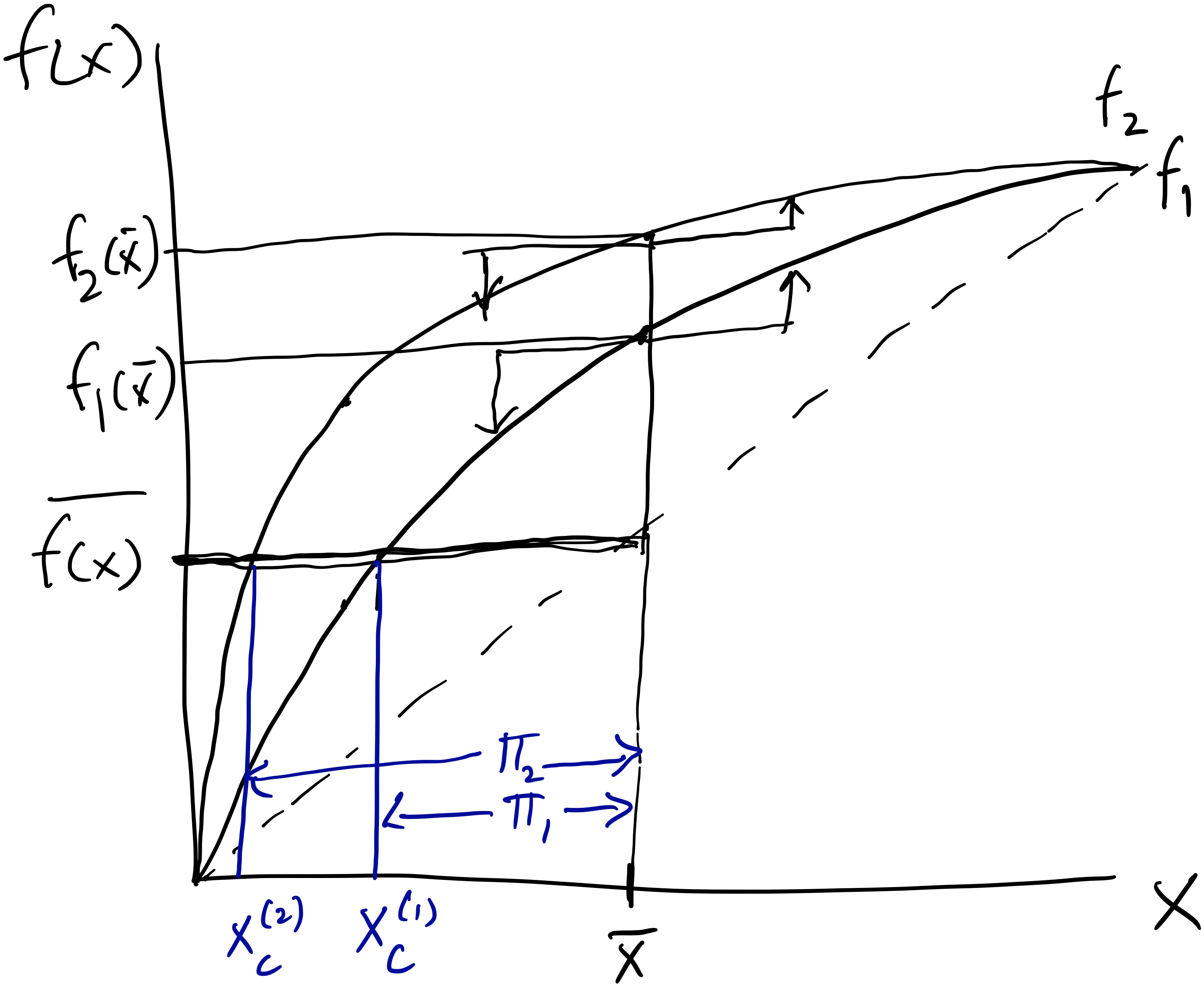
- Shows that variance is generally bad for fitness since $\frac{1}{2} f''(x) Var(x) < 0$



$\boxed{\text{Risk-Averse}}$



π = certainty premium



Arrow-Pratt Index of Absolute Risk Aversion

$$\boxed{A_f = -\frac{f''(x)}{f'(x)}}$$

RV ε

$$\underline{\mathbb{E}[f(x+\varepsilon)]} = \underline{f(x-\pi)} \qquad \begin{array}{l} \text{mean} = 0 \\ \boxed{\text{Var} = \sigma^2} \end{array}$$

2nd order Taylor series

1st order Taylor series

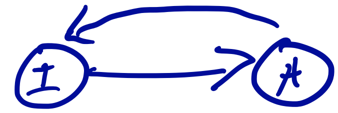
$$\mathbb{E}\left[f(x) + \cancel{\varepsilon f'(x)}^{\,0} + \cancel{\frac{\varepsilon^2}{2}}^{\,\text{Var}(x)} f''(x)\right] =$$

$$f(x) - \pi f'(x)$$

$$\cancel{f(x)} - \frac{f''(x)}{f'(x}\frac{\text{Var}(x)}{2} = \cancel{f(x)} + \pi \cancel{f'(x)}$$

$$\pi = -\frac{f''(x)}{f'(x)}\frac{\text{Var}(x)}{2} = \frac{A_f\,\sigma^2}{2}$$

Coale (1957)



Characteristic Equation

$$1 = \int_{\alpha}^{\beta} e^{-ra} \, l(a) \, m(a) \, da$$

Number of births at time t

$$B(t) = \int_{0}^{t} N(a,t) \, m(a) \, da + G$$

$$N(a,t) = B(t-a) \, l(a)$$

substitute!

$\beta \geq 50$

$$B(t) = \int_{\alpha}^{\beta} B(t-a)\, l(a) m(a)\, da$$

trial solution: $B(t) = Be^{rt}$

$$Be^{rt} = \int_{\alpha}^{\beta} Be^{r(t-a)} l(a) m(a)\, da =$$

$$\int_{\alpha}^{\beta} Be^{rt} e^{-ra} l(a) m(a)\, da$$

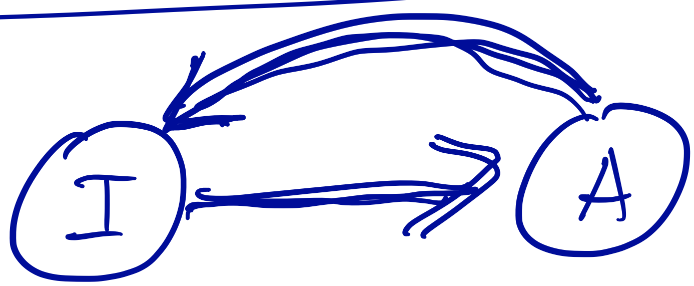
Divide both sides by Be^{rt}:

$$1 = \int_{\alpha}^{\beta} e^{-ra} l(a) m(a)\, da$$

Characteristic Equation

Euler - Lotka

$$1 = \int_{\alpha}^{\beta} e^{-ra}\, l(a)\, m(a)\, da$$



$$B(t) = \int_0^t N(a,t)\, m(a)\, da + G$$

$$N(a,t) = \underline{B(t-a)\, l(a)}$$

$\beta > 50$

$$B(t) = \int_{\alpha}^{\beta} B(t-a)\, l(a)\, m(a)\, da$$

$$B(t) = Be^{rt}$$

$$Be^{rt} = \int_{\alpha}^{\beta} Be^{r(t-a)}\, l(a)\, m(a)\, da$$

$$= \int_{\alpha}^{\beta} Be^{rt} e^{-ra}\, l(a)\, m(a)\, da$$

$$\boxed{1 = \int_{\alpha}^{\beta} e^{-ra}\, l(a)\, m(a)\, da}$$

$$B(t) = Be^{rt}$$

$$\underline{N(a,t)} = Be^{r(t-a)} \ell(a) =$$

$$Be^{rt} e^{-ra} \ell(a) = \underline{B(t) e^{-ra} \ell(a)}$$

$$\int_0^\infty \underline{N(a,t)}\, da = N(t) = \overbrace{B(t) \int_0^\infty e^{-ra} \ell(a)\, da}$$

$$\frac{B(t)}{N(t)} = \frac{\cancel{B(t)}}{\cancel{B(t)} \int_0^\infty e^{-ra} \ell(a)\, da}$$

$$\frac{B(t)}{N(t)} = \boxed{\frac{1}{\int_0^\infty e^{-ra} \, l(a) \, da} = b}$$

$$\frac{N(a,t)}{N(t)} = \frac{B(t)}{N(t)} e^{-ra} \, l(a)$$

$$\frac{N(a,t)}{N(t)} = \boxed{b e^{-ra} \, l(a) = c(a)}$$

$$1 = \int_{\alpha}^{\beta} e^{-ra}\, l(a)\, m(a)\, da$$

1. How many live births?

$$\psi(a) = \underline{l(a)\, m(a)}$$

net maternity function

$$R_0 = \int_\alpha^\beta l(a)\, m(a)\, da$$

Net Reproduction ~~Rate~~ Ratio

(NRR)

$$R_0 = e^{rT} \qquad T = \int_\alpha^\beta a\, e^{-ra}\, l(a)\, m(a)\, da$$

$$R_0 = 1$$

② What if $r = 0$

$e^0 = 1$ $\quad r = 0$

$$1 = \int_{\alpha}^{\beta} \underbrace{e^{-r\alpha}}_{=1} \, l(\alpha)\, m(\alpha)\, d\alpha$$

$$1 = \int_{\alpha}^{\beta} \underline{l(\alpha)\, m(\alpha)\, d\alpha}$$

- reduces to NRR
- equals 1 !

③ birth rate

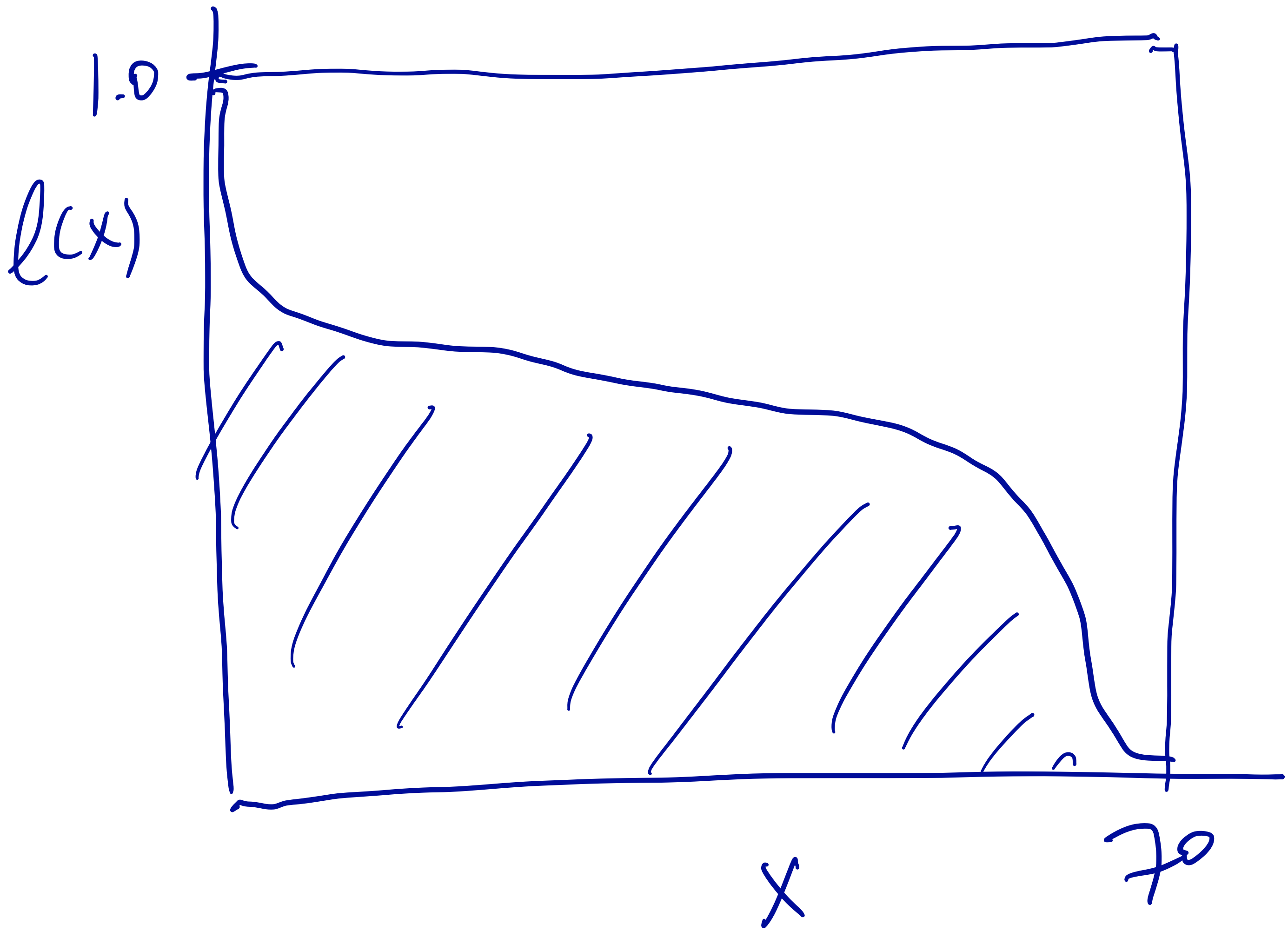
$$b = \frac{1}{\int_0^\infty \cancel{e^{-ra}} \, l(a)\, da} \quad 1 \quad e^0 = 1$$

$r = 0$

$$b = \frac{1}{\int_0^\infty l(a)\, da}$$

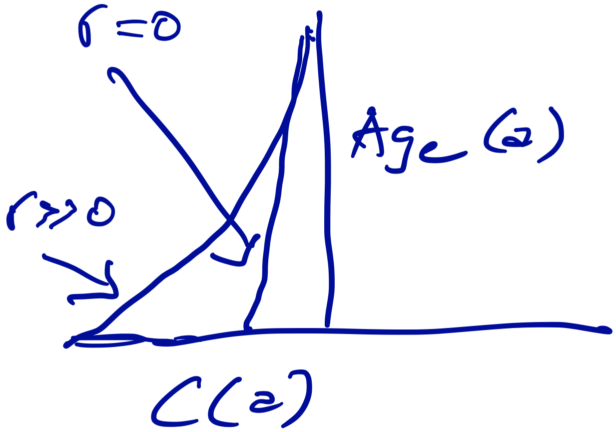
$$\boxed{\mathring{e}_0 b = 1}$$

$$\mathring{e}_0 b = \frac{\int_\alpha^\alpha l(a)\, da}{\int_\alpha^\beta l(a)\, da} = 1$$

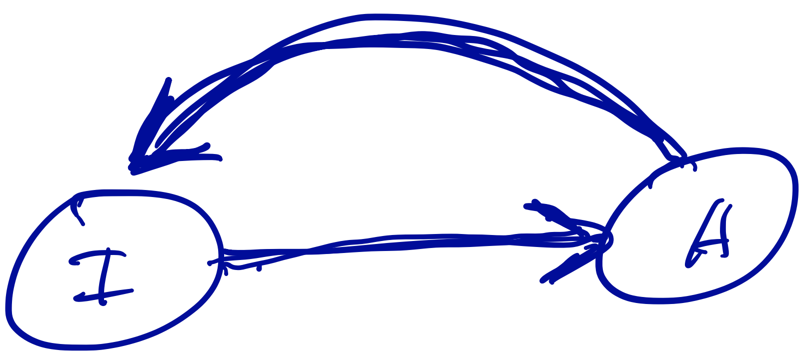


$$\mathring{e}_x = \int_x^\infty l(a)\,da$$

$$\boxed{1 = \int_{\alpha}^{\beta} e^{-ra} \underbrace{l(a)\, m(a)}_{\psi(a)}\, da} \qquad \boxed{r \geq 0}$$



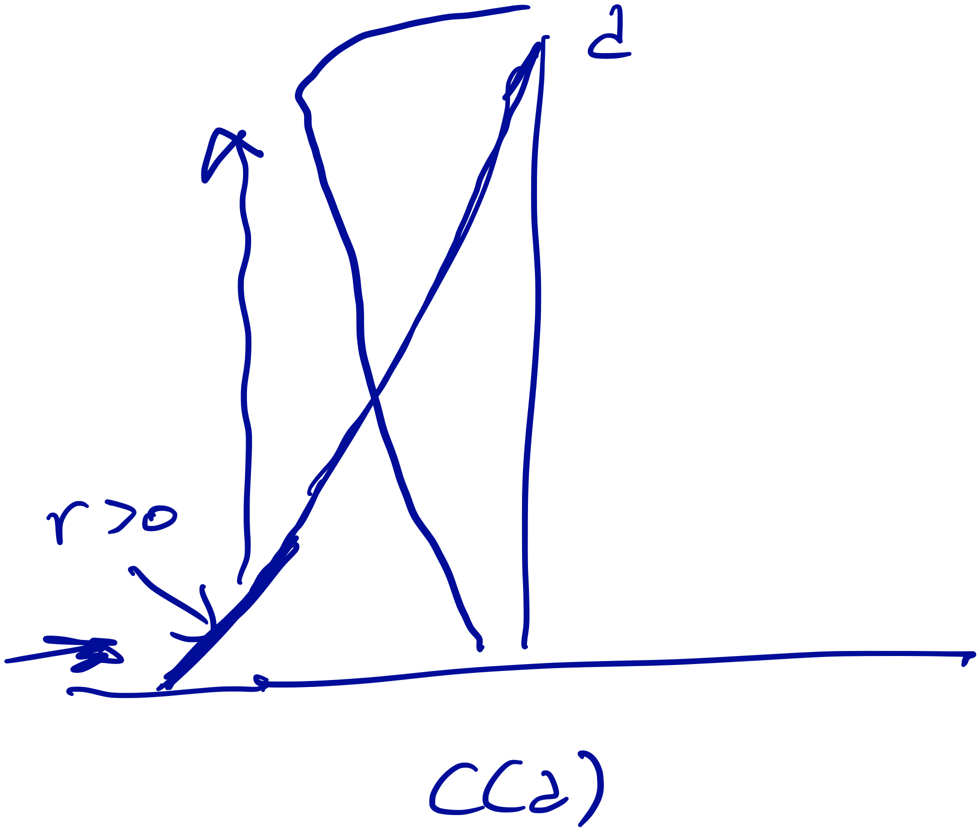
net maternity function



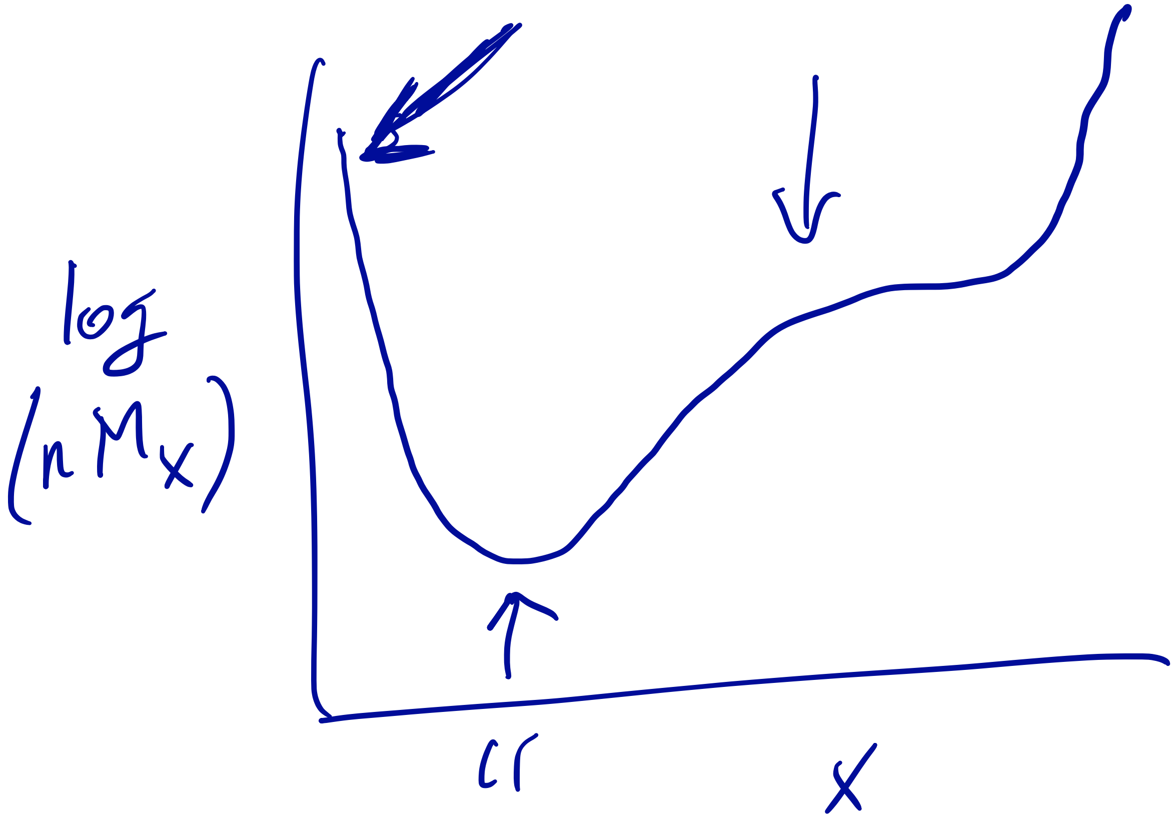
$$r = 0 \; : \; e^{-0a} = 1$$

$$\Rightarrow \; 1 = \int_{\alpha}^{\beta} \underbrace{l(a)\, m(a)}_{\psi(a)}\, da$$

<u>NRR</u> or R_0



Madagascar
1965
$\hat{e}_0 = 37$

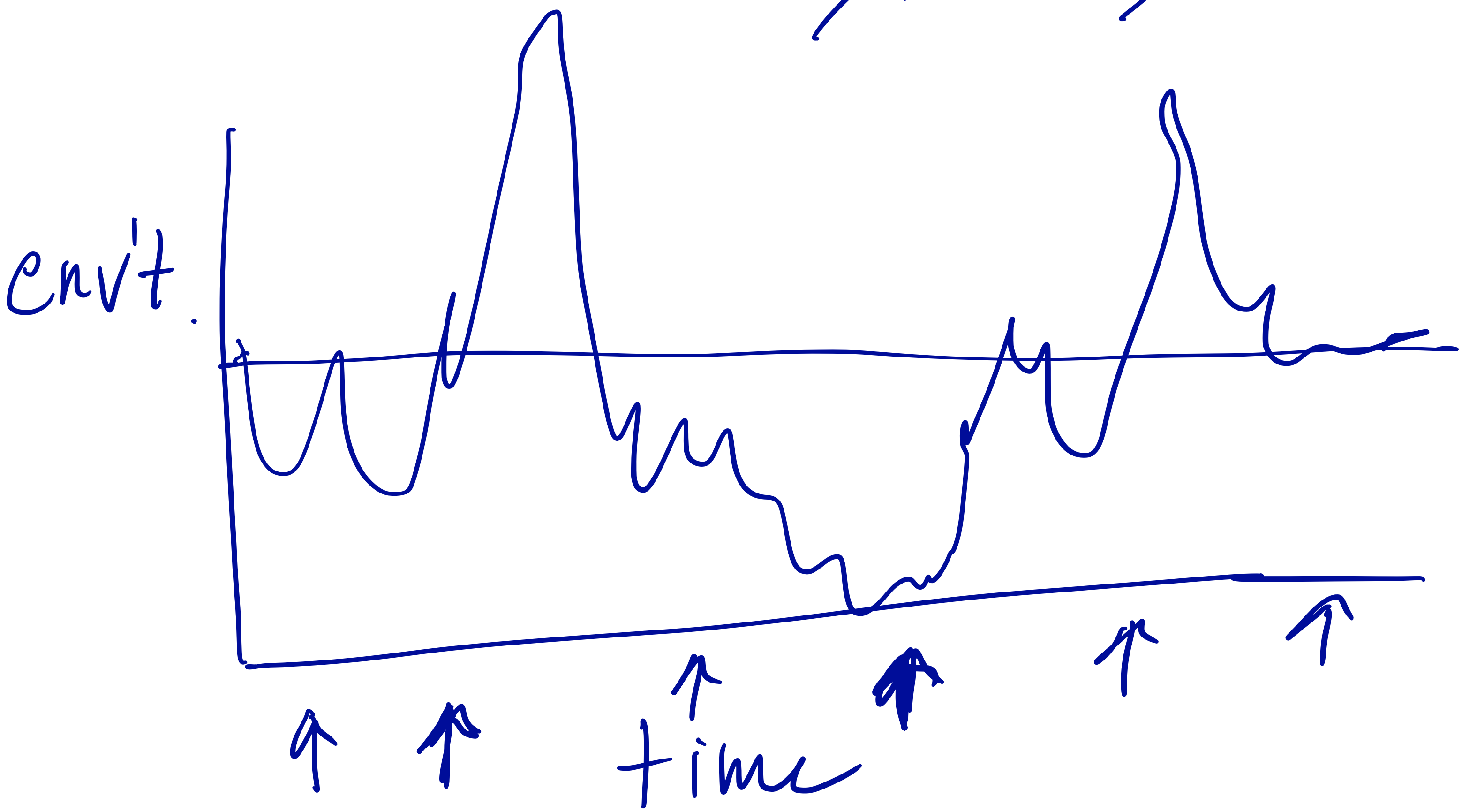


$r < 0$

$$1 = \int_\alpha^\beta \boxed{e^{-ra}}\, l(a)\, m(a)\, da$$

> 1

$$\cancel{-r\alpha} - r + \cancel{r\alpha}$$



$$1 = \sum e^{-r\alpha} l_a m_a$$

$$1 = e^{-r\alpha}\psi_\alpha + e^{-r\alpha+1}\psi_{\alpha+1}$$

$$e^{r\alpha} = \cancelto{1}{e^{r\alpha} e^{-r\alpha}}\psi_\alpha + \cancelto{e^{-r}}{e^{-r\alpha+1} e^{r\alpha}}\psi_{\alpha+1}$$

$$\boxed{1 = \sum_{\alpha}^{\omega} e^{-rx} l_x m_x}$$

$$1 = e^{-r\alpha}\psi_\alpha + e^{-r(\alpha+1)}\psi_{\alpha+1}$$

$$e^{r\alpha} = \underbrace{\cancel{e^{-r\alpha} e^{r\alpha}}}_{1}\psi_\alpha + \underbrace{\cancel{e^{-r(\alpha+1)} e^{r\alpha}}}_{e^{-r}}\psi_{\alpha+1}$$

$$e^{r\alpha} = \psi_\alpha + e^{-r}\psi_{\alpha+1}$$

$$\psi_\alpha = \overset{1}{\cancel{l_\alpha}} m_\alpha = b$$

$$e^{r\alpha} = b\left(1 + e^{-r} + e^{-2r} + \dots e^{-r(\omega-\alpha)}\right)$$

$$\frac{e^{r\alpha}}{b} = \frac{b}{b}\left(\frac{1-e^{-rn}}{1-e^{-r}}\right)$$

$$n = \omega - \alpha + 1$$

$$\frac{e^{r\alpha}}{b} = \frac{1-e^{-rn}}{1-e^{-r}}$$

$$\frac{e^{r\alpha}}{b} - \frac{e^{r\alpha}e^{-r}}{b} = 1 - be^{-rn}$$

$$e^{r\alpha} - e^{r(\alpha+1)} = b - be^{-rn}$$

$$\boxed{1 = be^{-r\alpha} - be^{-r(\alpha+n)} + e^{-r}}$$

$$r_s = \log\left[\frac{N_{t+1}}{N_t}\right] =$$

$$\log\left[\frac{b_s \cancel{N_t}}{\cancel{N_t}}\right]$$

$$\boxed{r_s = \log(b_s)}$$

Cole's r_{max}:

$n+\alpha = \omega + 1$

$$1 = e^{-r} + be^{-r\alpha} - \underbrace{\boxed{be^{-r(n+\alpha)}}}_{0}$$

$\alpha = 1$

$\omega = \infty$

$$1 = e^{-r} + be^{-r}$$

$$1 = e^{-r}(1+b)$$

$$0 = -r + \log(b+1)$$

$$r = \log(b+1)$$

$$r_s = \log(b)$$

$$1 = \sum_{\alpha}^{\omega} e^{-rx} l_x m_x$$

$$1 = e^{-r\alpha}\psi_\alpha + e^{-r(\alpha+1)}\psi_{\alpha+1}$$

$$e^{r\alpha} = \underbrace{\cancel{e^{-r\alpha} e^{r\alpha}}}_{1}\psi_\alpha + \underbrace{\cancel{e^{-r(\alpha+1)} e^{r\alpha}}}_{e^{-r}}\psi_{\alpha+1}$$

$$e^{r\alpha} = \psi_\alpha + e^{-r}\psi_{\alpha+1}$$

$$e^{r\alpha} = b\left(1 + e^{-r} + e^{-2r} + \dots + e^{-r(\omega-\alpha)}\right)$$

$$\frac{e^{r\alpha}}{b} = \frac{b}{b}\left(\frac{1-e^{-rn}}{1-e^{-r}}\right)$$

$$n = w - \alpha + 1$$

$$\frac{e^{r\alpha}}{b} - \frac{e^{r\alpha - r}}{b} = 1 - e^{-rn}$$

$$e^{r\alpha} - e^{r(\alpha-1)} = b - be^{-rn}$$

$$+ e^{r(\alpha-1)}$$

$$0$$

$$\boxed{1 = be^{-r\alpha} - be^{-r(\alpha+n)} + e^{-r}}$$

Charnov + Schaffer (1973)

$$\sum_{k=0}^{\infty} a r^k = \frac{a}{1-r}$$

— definition of an infinite geometric series

P = survival prob K = AFR

$c(K)$ = recruitment fraction

$$1 = B_i\, c(K) \left[\frac{1}{\lambda^K} + \frac{P}{\lambda^{K+1}} + \frac{P^2}{\lambda^{K+2}} + \dots \right]$$

multiply by $\frac{\lambda^K}{\lambda^K}$

$$1 = \frac{B_i\, c(K)}{\lambda^K} \left[1 + \frac{P}{\lambda} + \frac{P^2}{\lambda^2} + \frac{P^3}{\lambda^3} + \dots \right]$$

The ratio is P/λ

$$1 = \frac{B_i C(k)}{\lambda^k}\left[\frac{1}{1-P/\lambda}\right]$$

Semelparous

$$1 = \frac{B_s C(k)}{\lambda^k} \qquad \lambda^k = B_s C(k)$$

substitute

$$B_s C(k) = B_i C(k)\left[\frac{1}{1-P/\lambda}\right]$$

$$(1-P/\lambda) B_s \cancel{C/k} = B_i \cancel{C/k} \qquad \boxed{\frac{B_i}{B_s} = 1-P/\lambda}$$

$$N_{t+1} = \lambda N_t \qquad \lambda = e^r$$

Semelparous

$$N_{t+1} = S_j b_s N_t$$

$$\boxed{\lambda_s = S_j b_s}$$

iteroparous

$$N_{t+1} = S_j b_i N_t + S_a N_t$$

$$\boxed{\lambda_i = S_j b_i + S_a}$$

$$\lambda_s = \lambda_i$$

$$\frac{\cancel{s_j} b_s}{\cancel{s_j}} = \frac{\cancel{s_j} b_i}{\cancel{s_j}} + \frac{s_d}{s_j}$$

$$\boxed{b_s = b_i + \frac{s_d}{s_j}}$$

Sue Weller:
713-854-6703

$$\sum_{k=0}^{\infty} a r^k = \frac{a}{1-r}$$

$r = P/\lambda$

Characteristic Equation for Iteroparous Life History

$$1 = b_i S_\alpha \left[\frac{1}{\lambda^\alpha} + \frac{P}{\lambda^{\alpha+1}} + \frac{P^2}{\lambda^{\alpha+2}} + \dots \right]$$

$$\frac{\lambda^\alpha}{\lambda^\alpha} = 1$$

$$1 = \frac{b_i S_\alpha}{\lambda^\alpha} \left[1 + \frac{P}{\lambda} + \frac{P^2}{\lambda^2} + \frac{P^3}{\lambda^3} + \dots \right]$$

$$1 = \frac{b_i S_\alpha}{\lambda^\alpha}\left[\frac{1}{1 - P/\lambda}\right]$$

Characteristic Equation for Semelparous Life History

$$1 = \frac{b_s S_\alpha}{\lambda^\alpha}$$

$$\lambda^\alpha = \boxed{b_s S_\alpha}$$

$$1 = \frac{b_i S_\alpha}{b_s S_\alpha}\left[\frac{1}{1 - P/\lambda}\right]$$

$$1 = \frac{b_i S_\alpha}{b_s S_\alpha}\left[\frac{1}{1-P/\lambda}\right]$$

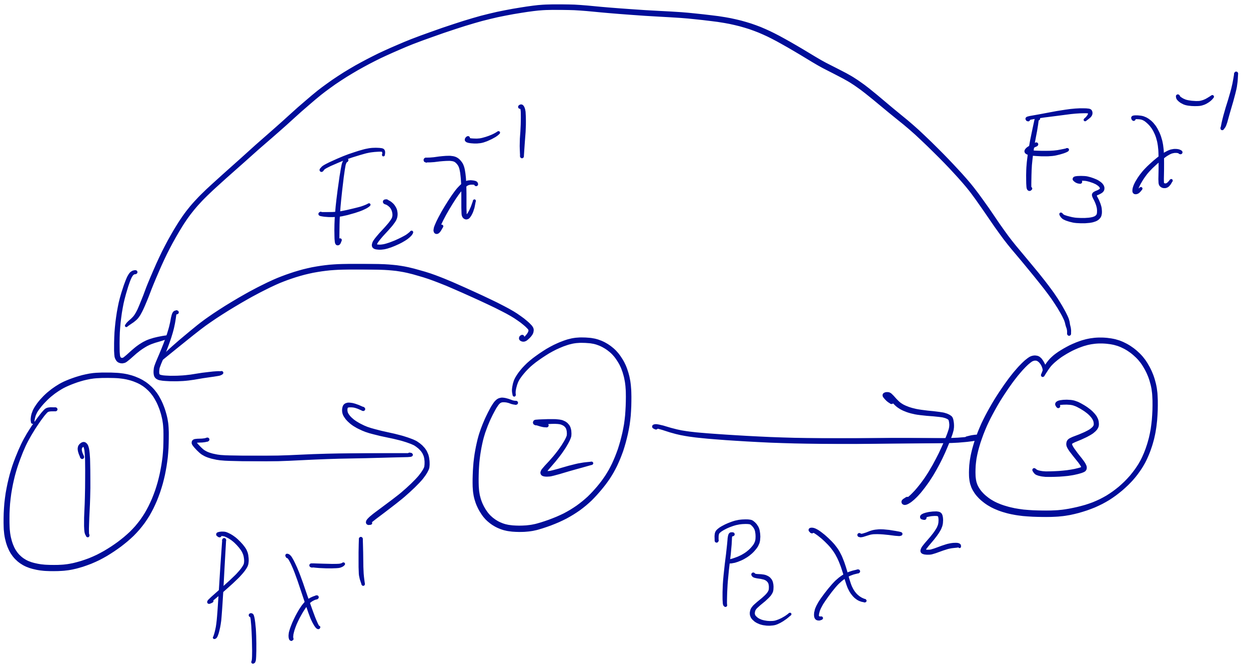
$$b_s S_\alpha = b_i S_\alpha \left[1-P/\lambda\right]$$

$$\frac{(1-P/\lambda)\, b_s \cancel{S_\alpha}}{b_s} = \frac{b_i}{b_s}\cancel{S_\alpha}$$

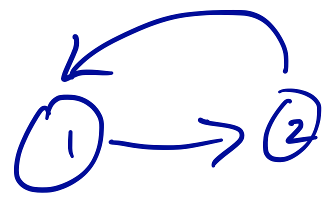
$$\boxed{\frac{b_i}{b_s} = 1 - \boxed{\frac{P}{\lambda}}}$$

$1 \geq P \geq 0$

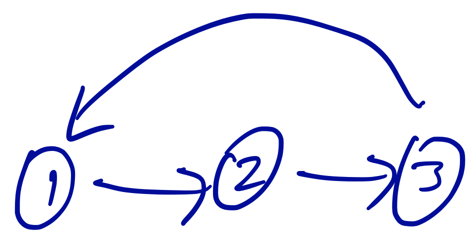
$\lambda \geq 1$



$$L^{(1)} = P_1 F_2 \lambda^{-2}$$



$$L^{(2)} \quad P_1 P_2 F_3 \lambda^{-3}$$

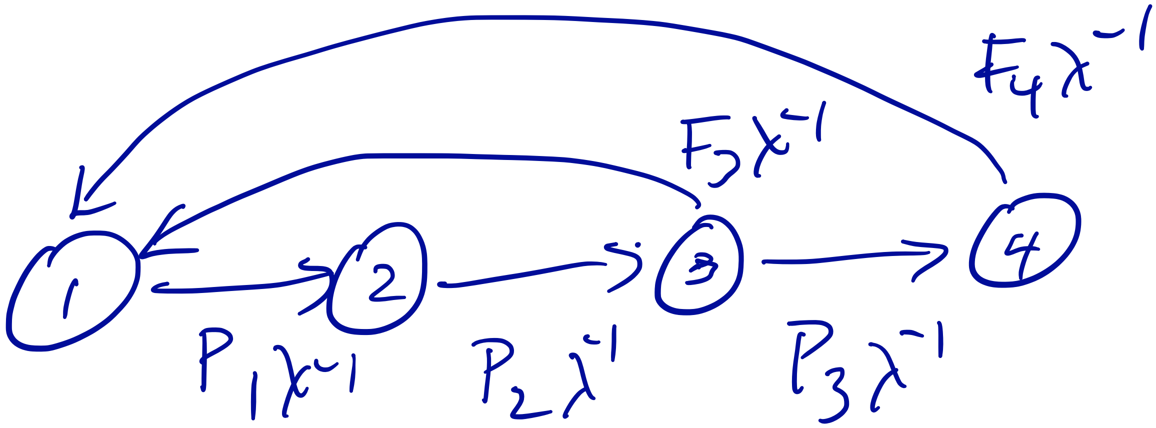


Characteristic Equation:

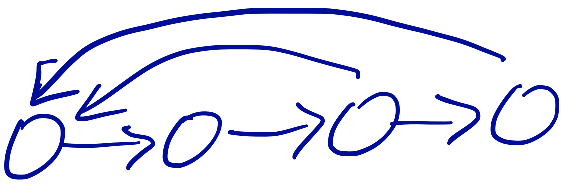
$$1 = L^{(1)} + L^{(2)}$$

$$\boxed{1 = P_1 F_2 \lambda^{-2} + P_1 P_2 F_3 \lambda^{-3}}$$

Reproductive Value

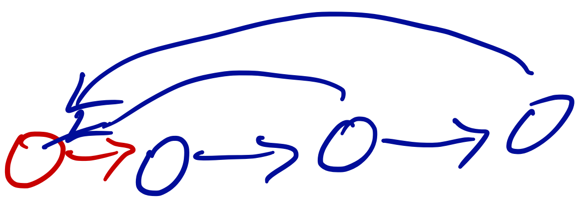


V_1



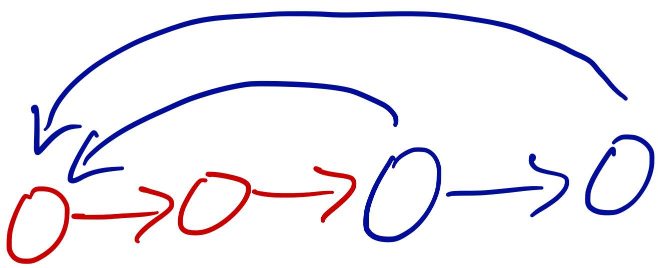
$= 1$

V_2



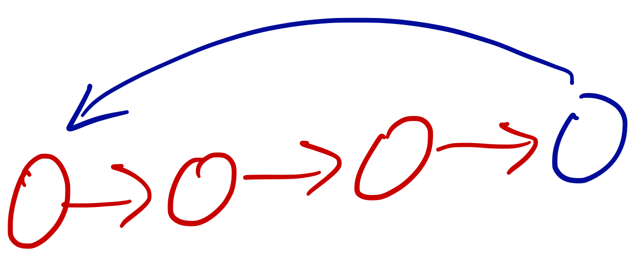
$= P_2F_3\lambda^{-2} + P_2P_3F_4\lambda^{-3}$

V_3



$= F_3\lambda^{-1} + P_3F_4\lambda^{-2}$

V_4



$= F_4\lambda^{-1}$

$$\begin{tikzcd}
1 \arrow[r, "P_1\lambda^{-1}"'] & 2 \arrow[r, "P_2\lambda^{-1}"'] & 3 \arrow[r, "P_3\lambda^{-1}"'] \arrow[ll, bend right, "F_3\lambda^{-1}"'] & 4 \arrow[lll, bend right=50, "F_4\lambda^{-1}"']
\end{tikzcd}$$

$u_1 \quad \circ \to \circ \to \circ \to \circ \quad = \quad 1$

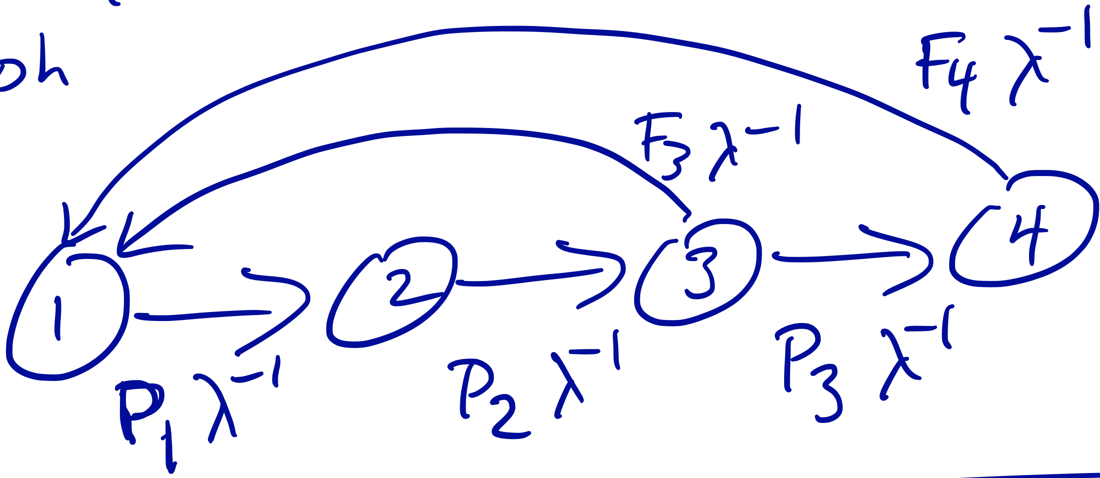
$u_2 \quad \circ \to \circ \to \circ \to \circ \quad = P_1\lambda^{-1}$

$u_3 \quad \circ \to \circ \to \circ \to \circ \quad = P_1P_2\lambda^{-2}$

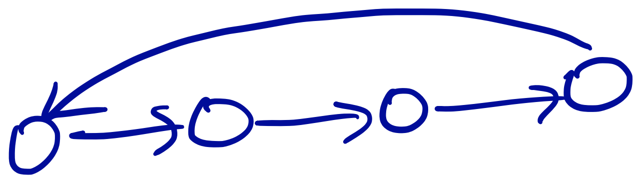
$u_4 \quad \circ \to \circ \to \circ \to \circ \quad = P_1P_2P_3\lambda^{-3}$

Z-transformed life-cycle graph

Caswell (2001)

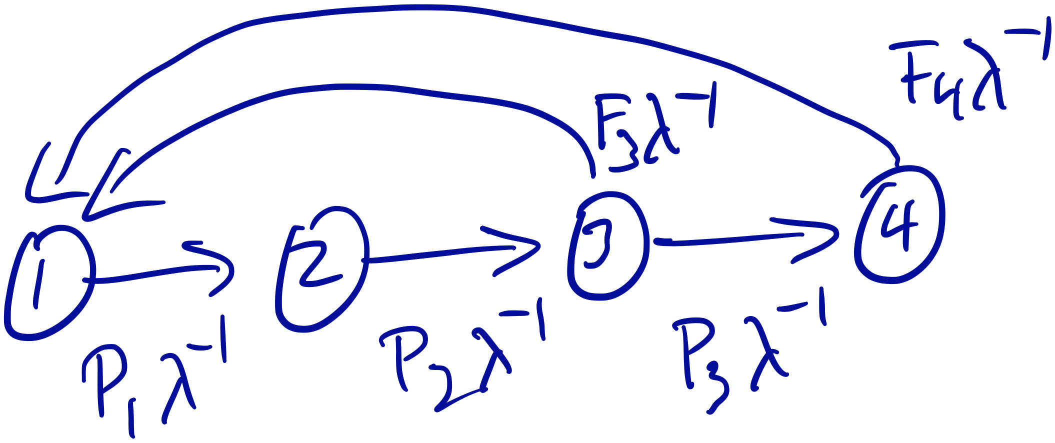


$L^{(1)}$:  $= \underline{P_1 P_2 F_3 \lambda^{-3}}$

$L^{(2)}$:  $= \underline{P_1 P_2 P_3 F_4 \lambda^{-4}}$

$$1 = \sum L^{(i)}$$

$$\boxed{1 = P_1 P_2 F_3 \lambda^{-3} + P_1 P_2 P_3 F_4 \lambda^{-4}}$$

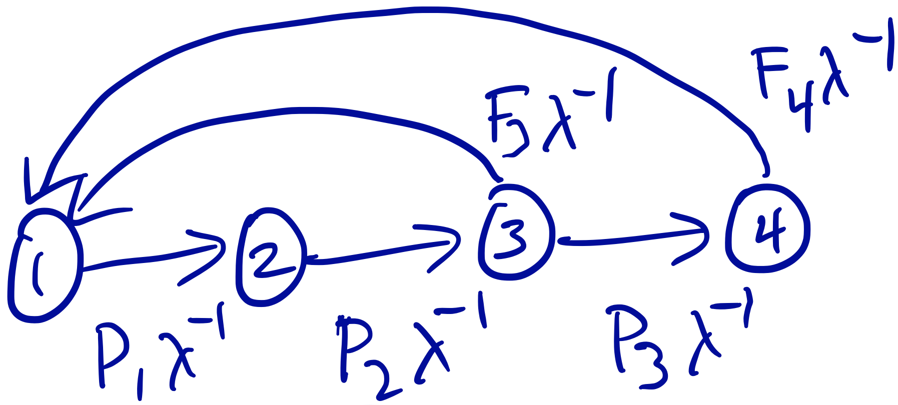


$$u_1 \quad O \to O \to O \to O \quad = 1$$

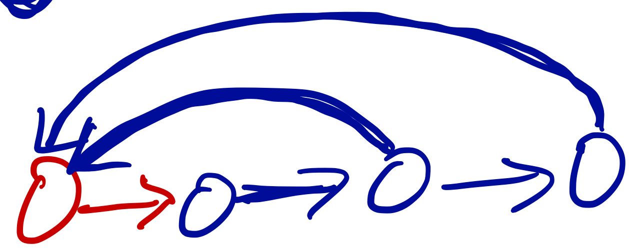
$$u_2 \quad O \to O \to O \to O \quad = P_1\lambda^{-1}$$

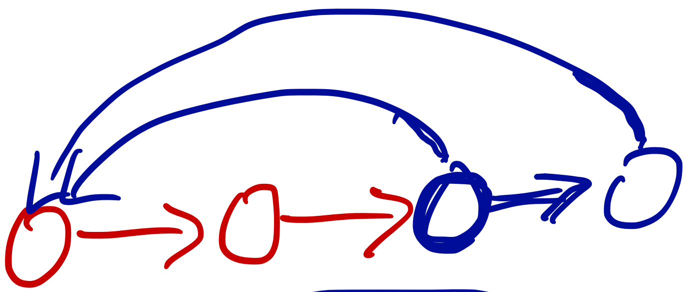
$$u_3 \quad O \to O \to O \to O \quad = P_1 P_2 \lambda^{-2}$$

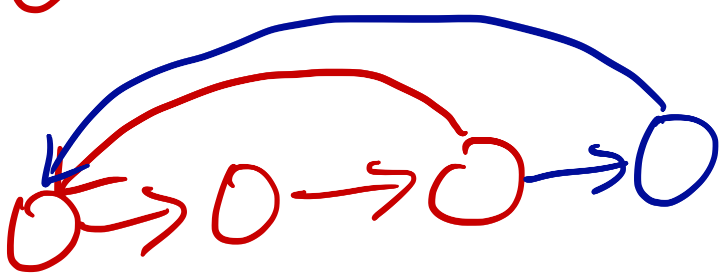
$$u_4 \quad O \to O \to O \to O \quad = P_1 P_2 P_3 \lambda^{-3}$$



V_1  $= 1$

V_2  $= P_2F_3\lambda^{-2} + P_2P_3F_4\lambda^{-3}$

V_3  $= F_3\lambda^{-1} + P_3F_4\lambda^{-2}$

V_4  $= F_4\lambda^{-1}$

$$R_0 = NRR = \int_\alpha^\beta l(x)\,m(x)\,dx$$

$$\boxed{R_0 = e^{rT}}$$

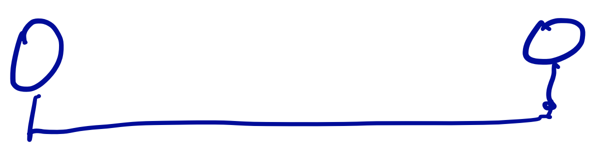
$$R_0 \equiv \lambda$$

r = intrinsic rate of increase

T = generation time

— mean age of childbearing

$$T = A_B = \int_\alpha^\beta x\,e^{-rx}\,l(x)\,m(x)\,dx$$

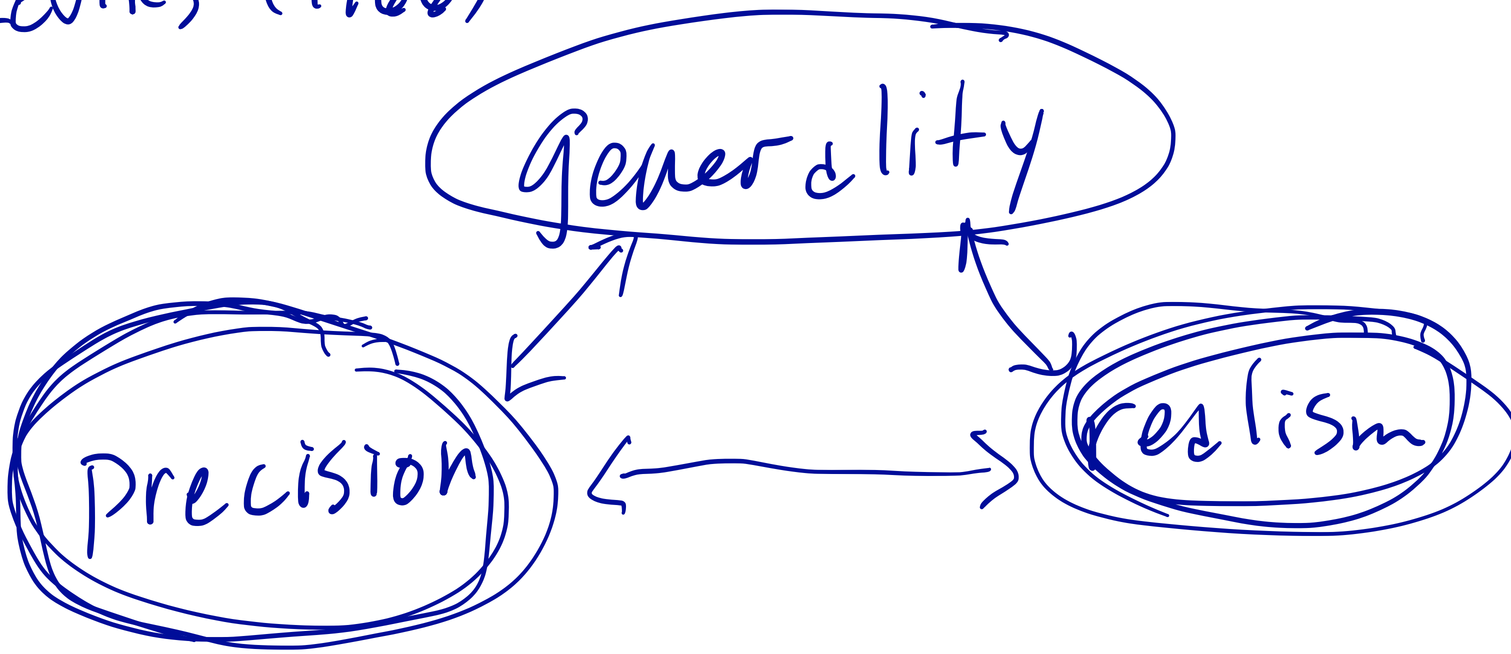


T

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

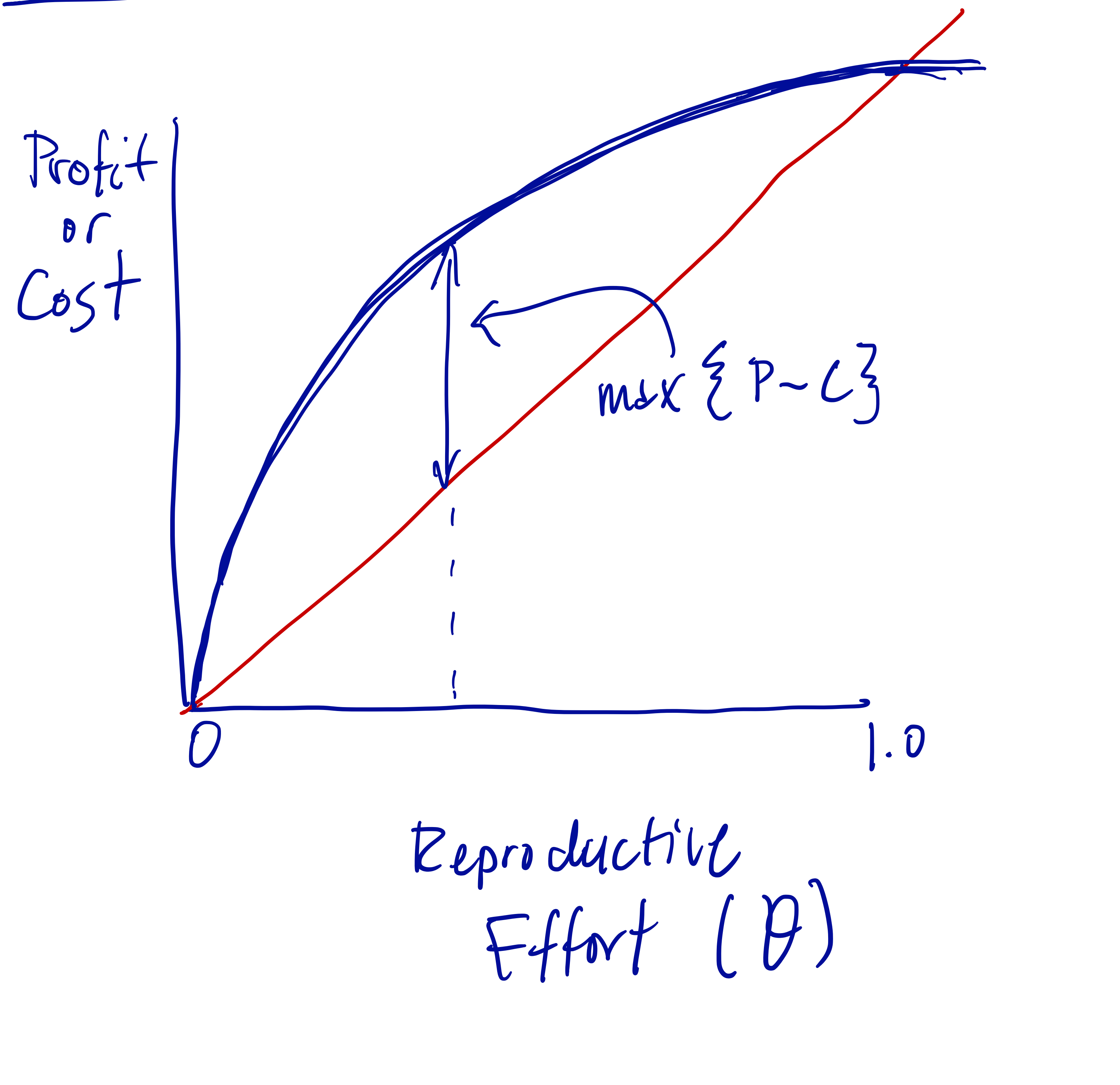
$$\lambda = \frac{N_{t+1}}{N_t}$$

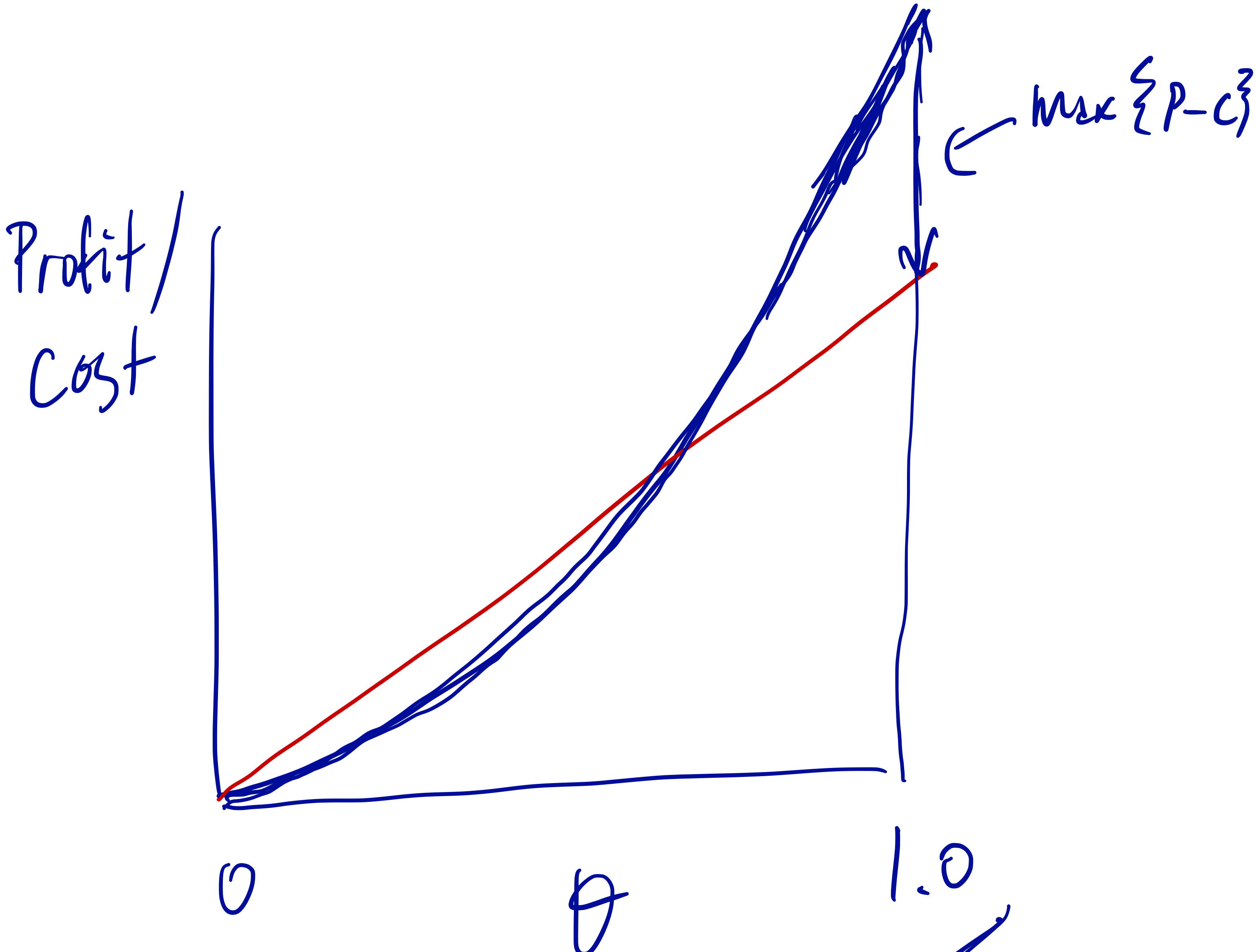
Levins (1966)



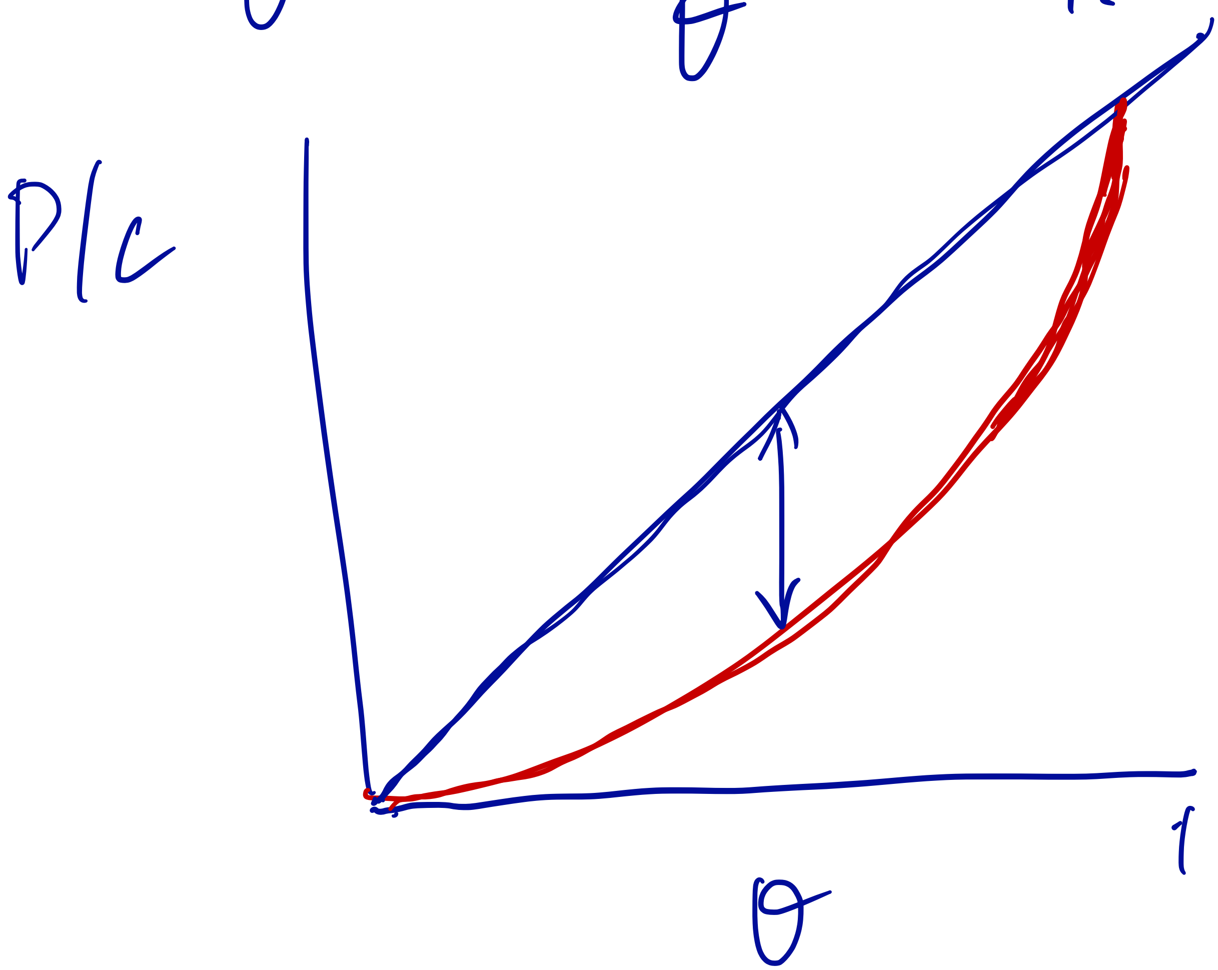
Concave $\Rightarrow$ $f''(x) < 0$

Convex $\Rightarrow$ $f''(x) > 0$





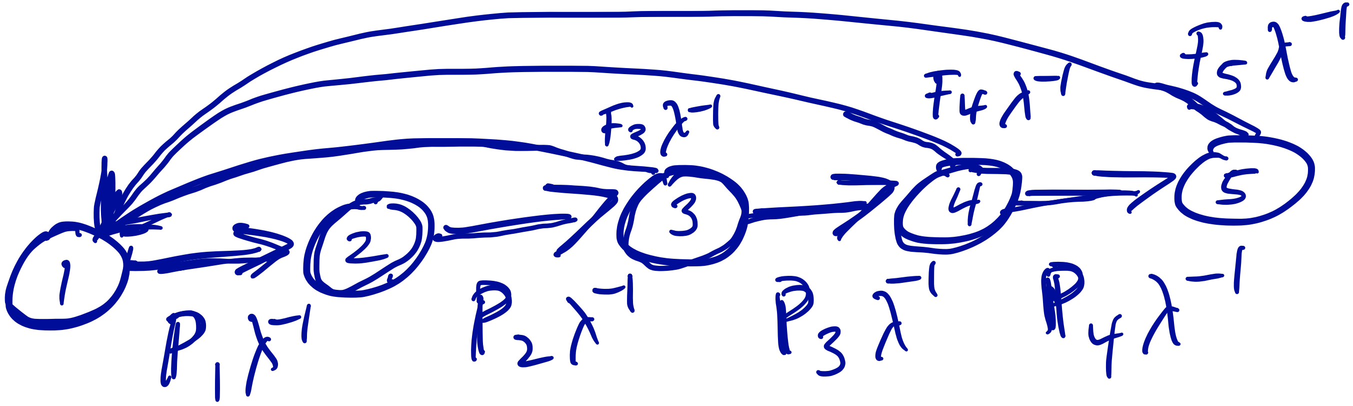
Profit/
Cost
max{P−C}
0
θ
1.0



P/C
θ
1

$$\boxed{1 = \sum_{x=1}^{n} e^{-rx} \underline{l_x} \, \underline{m_x}}$$

$$\boxed{\begin{aligned} l_x &= f(\theta, \psi) \\ m_x &= g(\theta, \psi) \end{aligned}}$$



$$v_1 = 1$$

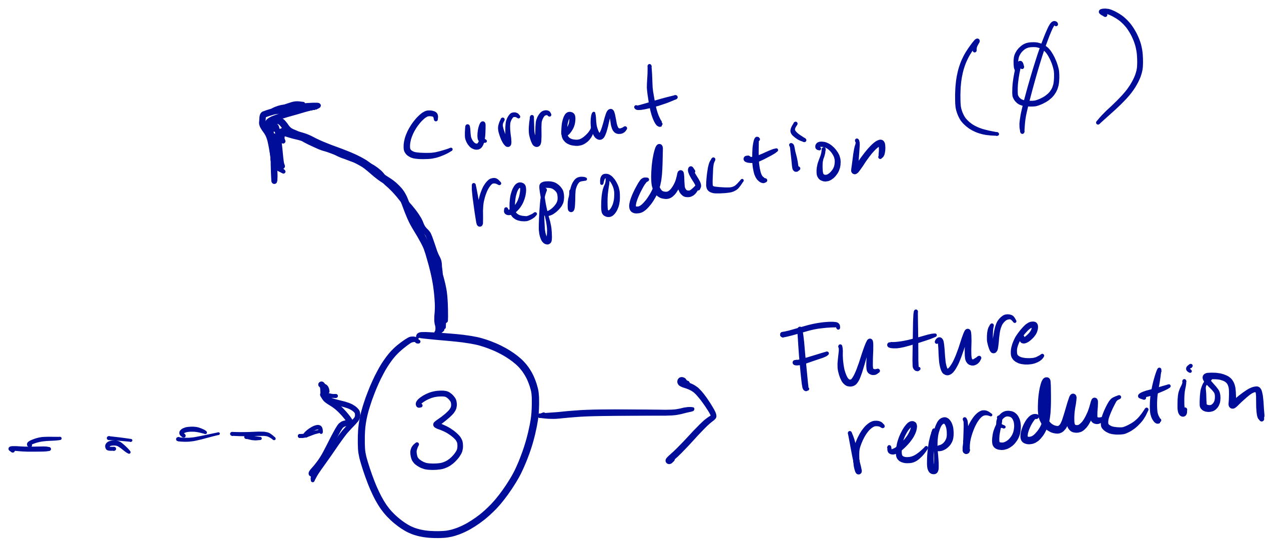
$$v_2 = P_2 F_3 \lambda^{-2} + P_2 P_3 F_4 \lambda^{-3} + P_2 P_3 P_4 F_5 \lambda^{-4}$$

$$v_3 = F_3 \lambda^{-1} + P_3 F_4 \lambda^{-2} + P_3 P_4 F_5 \lambda^{-3}$$

$$v_4 = F_4 \lambda^{-1} + P_4 F_5 \lambda^{-2}$$

$$v_5 = F_5 \lambda^{-1}$$

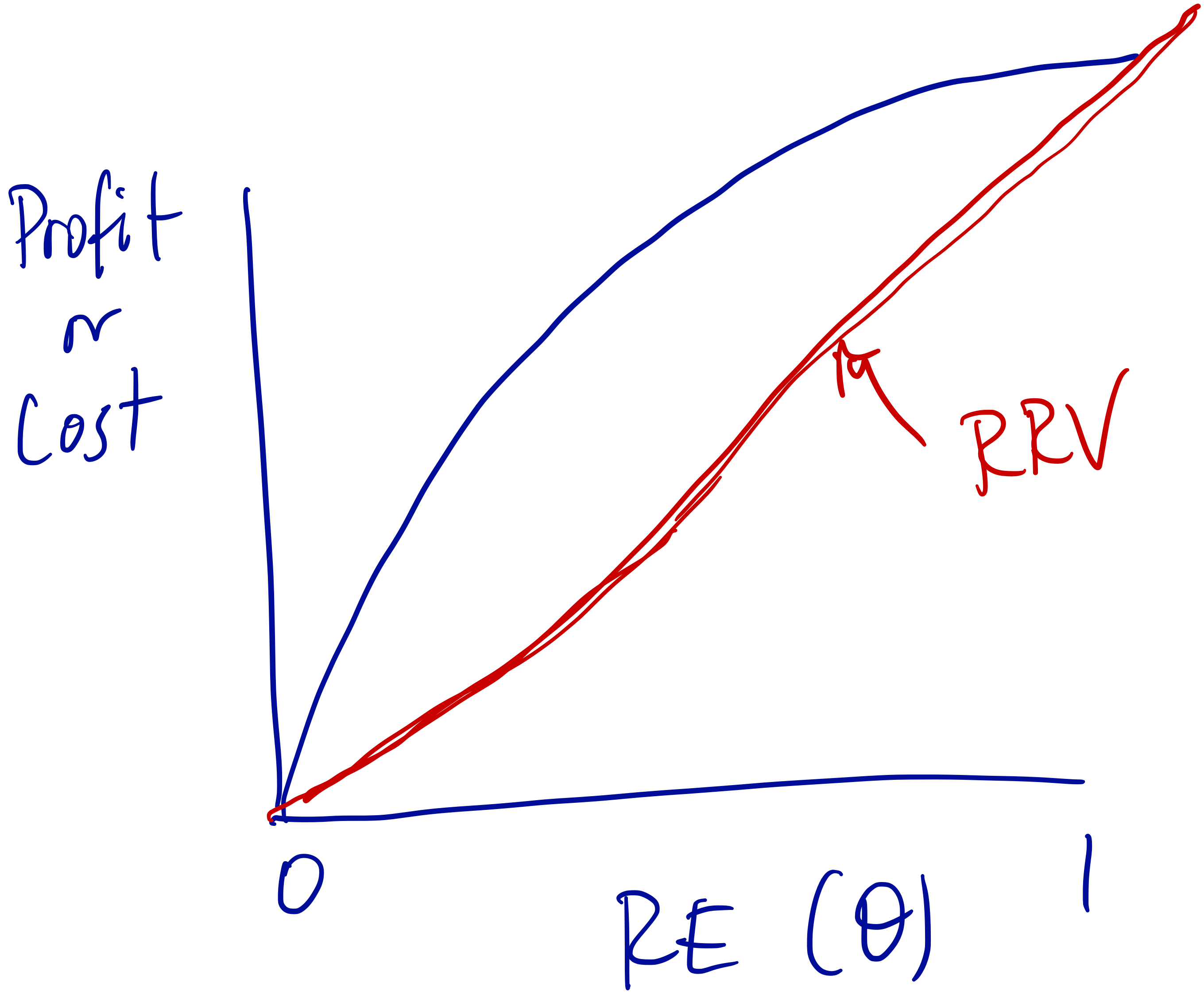
$$V_3 = F_3\lambda^{-1} + P_3F_4\lambda^{-2} + P_3P_4F_5\lambda^{-3}$$



$$V_3 = \phi_3 + RRV_3$$

$$\phi_3 = \boxed{F_3\lambda^{-1}}$$

$$RRV_3 = \underline{P_3F_4\lambda^{-2}} + \underline{P_3P_4F_5\lambda^{-3}}$$


Profit
or
Cost
RRV
0
1
RE (θ)

Stationary $(r=0)$ $NRR = e^{rT}$

$$\int_0^{\beta} \ell(x)\, m(x)\, dx = 1 \quad \leftarrow NRR$$

$$\int_a^{\beta} \frac{\ell(x)}{\ell(a)}\, m(x)\, dx = V(a)$$

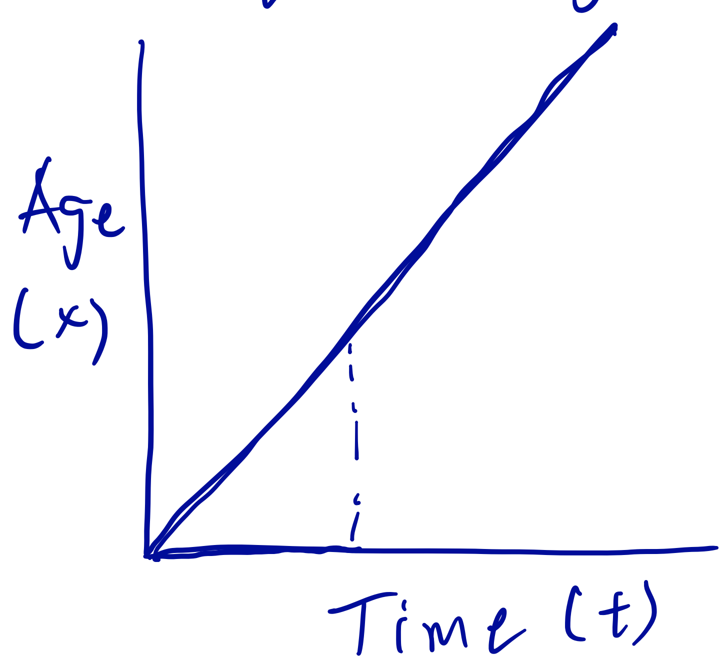
Non-Stationary $(r>0)$

$0 \qquad\qquad t$

$N_0 \qquad\qquad N_0 e^{rt}$

$$\boxed{e^{rx}}$$

Lexis Diagram



$$V(a) = \int_a^\beta e^{-r(x-a)} \frac{\ell(x)}{\ell(a)} m(x)\, dx$$

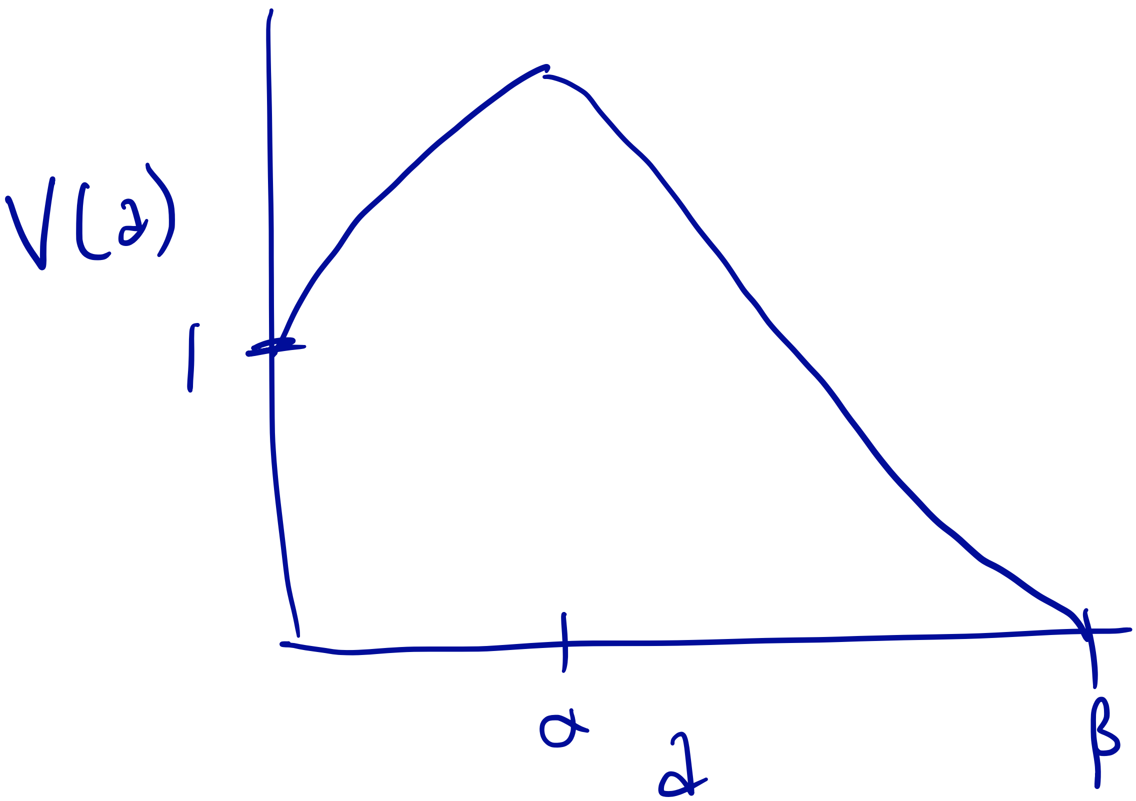
$$e^{-r(x-a)} = e^{-rx} e^{ra}$$

$$= \int_a^\beta e^{-rx} e^{ra} \frac{\ell(x)}{\ell(a)} m(x)\, dx$$

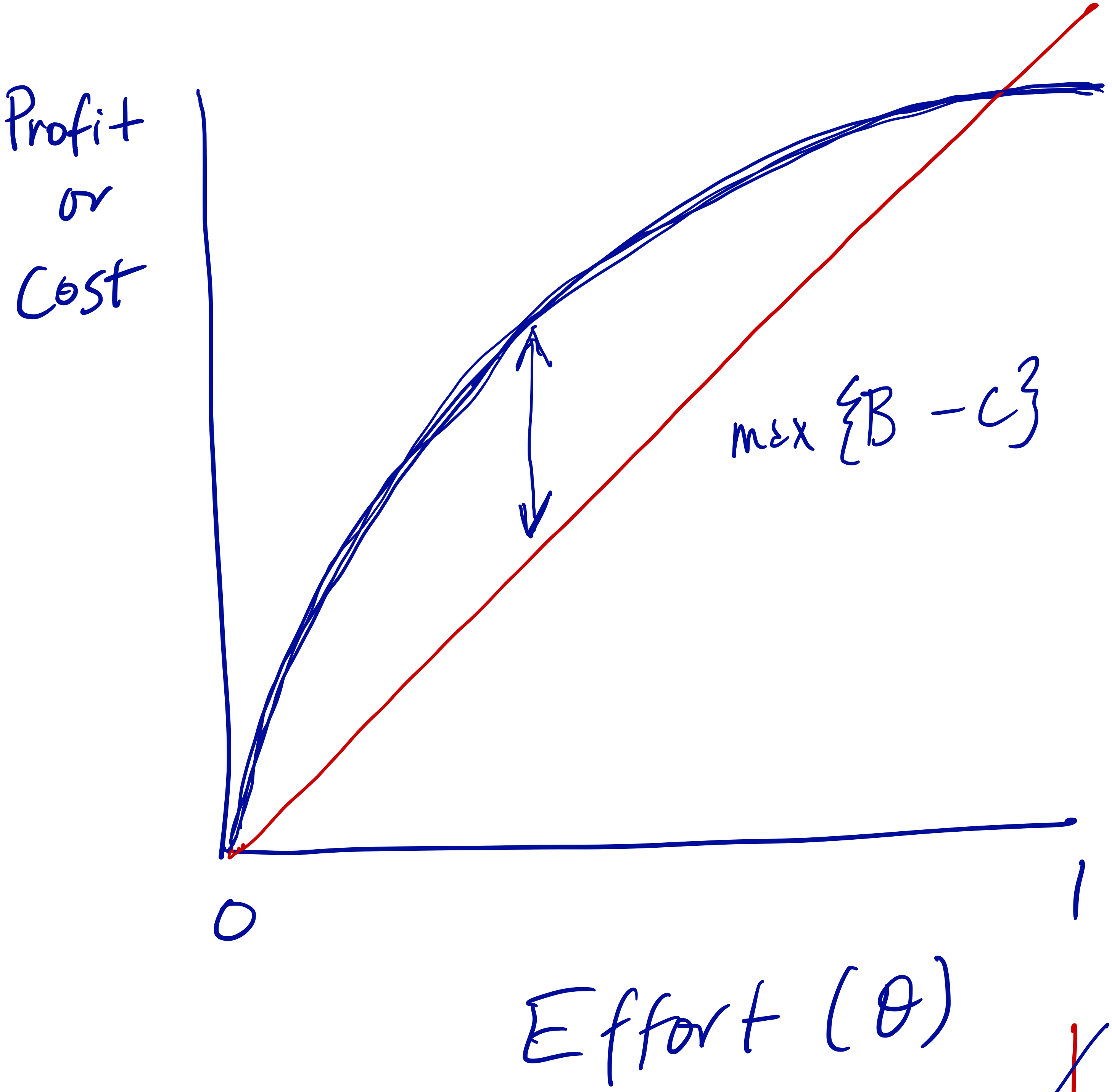
$$\boxed{V(a) = \frac{e^{ra}}{\ell(a)} \int_a^\beta e^{-rx} \ell(x) \underline{m(x)}\, dx}$$

< 1

$$V(0) = 1$$

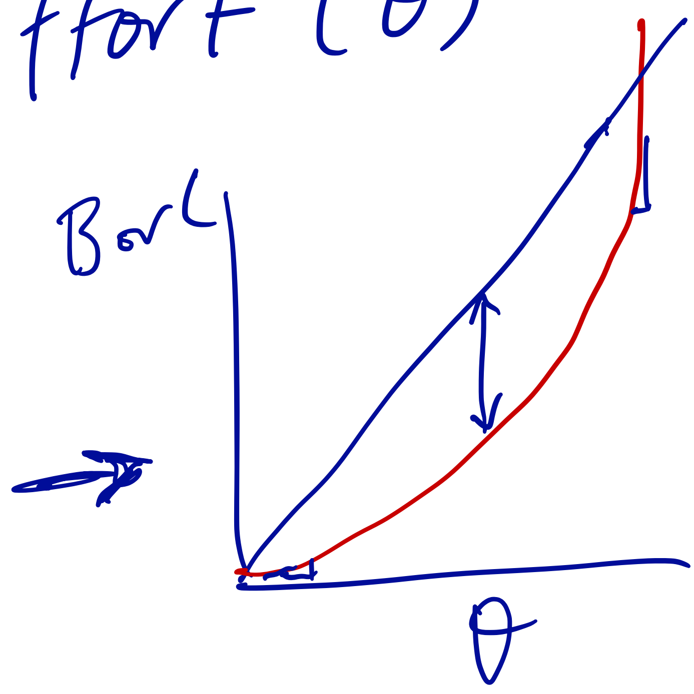


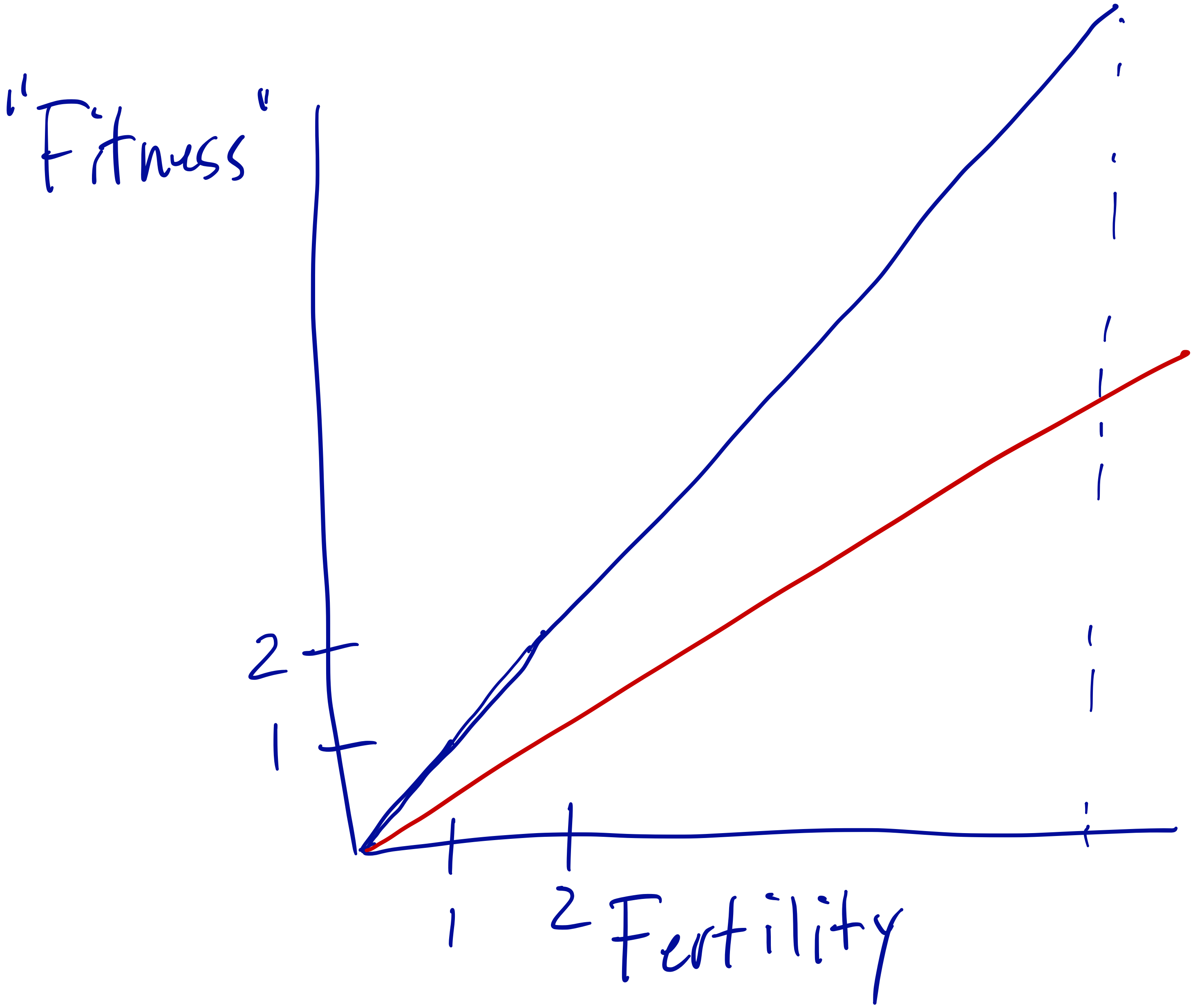
V(λ)
1
α
λ
β



$P'(\theta) > 0$

$P''(\theta) < 0$

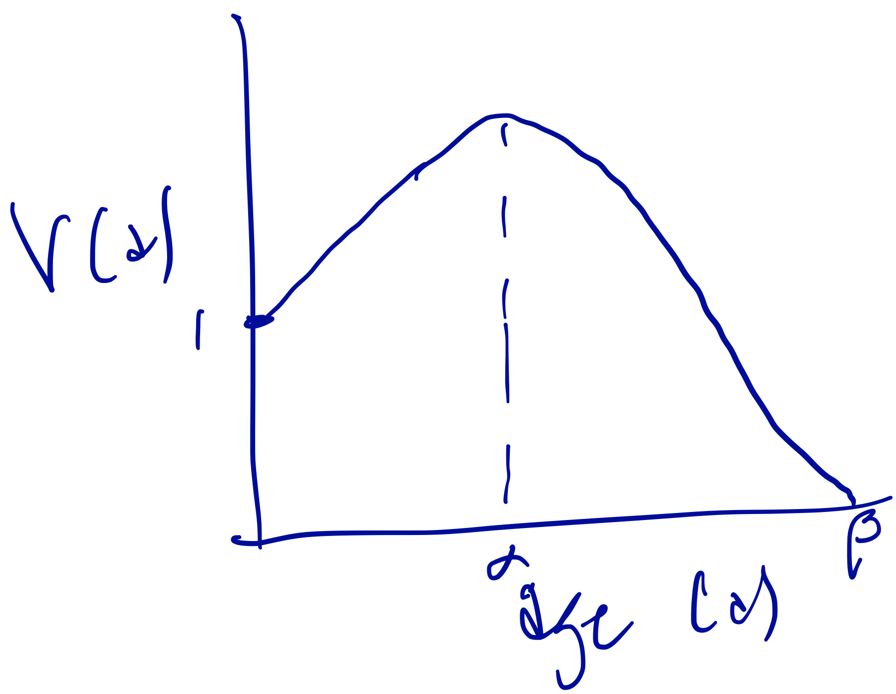




- Fertility
- Fecundity
- Fecundability

$$\underline{V(a)} = \frac{e^{ra}}{l(a)} \int_{a>\alpha}^{\beta} \underline{e^{-rx} l(x) m(x) dx}$$

$$\frac{a = 0}{\begin{gathered} e^{ra} = 1 \\ l(a) = 1 \end{gathered}} \qquad \frac{a > 0}{\begin{gathered} e^{ra} > 1 \\ l(a) < 1 \end{gathered}}$$



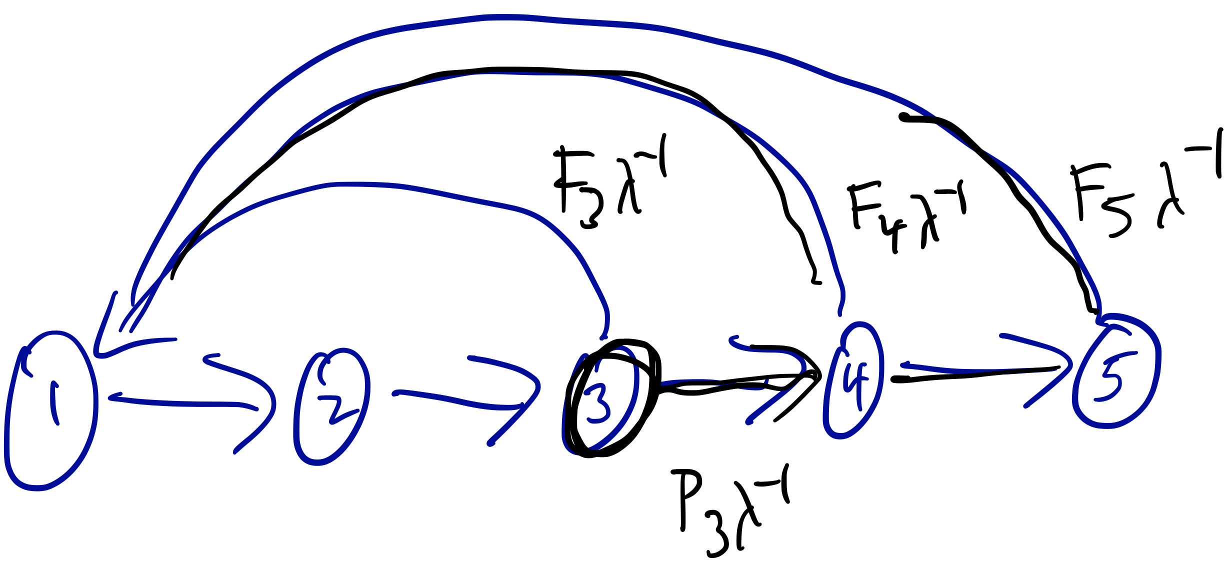
$\boxed{1930}$

$V(a) \approx 1 + r$

Williams (1966)

$$\boxed{RV_d = \psi_d + RRV_d}$$

Fertility



$$RV_3 = \underbrace{F_3\lambda^{-1}}_{\psi} + \underbrace{\left[P_3F_4\lambda^{-2} + P_3P_4F_5\lambda^{-3}\right]}_{RRV}$$

$$\lambda_g = B(1+s) + P$$

$$\lambda_b = B(1-s) + P$$

$$BP + \cancel{BPs} + BP - \cancel{BPs}$$

$$B^2(1-s^2) + BP(1+s) + BP(1-s) + P^2$$

$$B^2(1-s^2) + 2BP + P^2$$

$$B^2 - B^2s^2 + 2BP + P^2$$

$$B^2 + 2BP + P^2 - B^2s^2$$

$$\boxed{\bar{\lambda}^2 = (B+P)^2 - B^2s^2}$$

Schaffer (1974)

$$\lambda_g = B + P(1+s)$$

$$\lambda_b = B + P(1-s)$$

$$B^2 + BP - \cancel{BP}s + BP + \cancel{BP}s + P^2(1-s^2)$$

$$B^2 + 2BP + P^2 - P^2s^2$$

$$\boxed{\bar{\lambda}^2 = (B+P)^2 - P^2s^2}$$

$$\bar{\lambda}^2 = (B+P)^2 - s^2 B^2$$

$$\frac{d\bar{\lambda}^2}{dE} = 2(B+P)(B'+P') - 2s^2 B B' = 0$$

$$\cancel{2}(B+P)(B'+P') = \cancel{2}s^2 B B'$$

$$BB' + BP' + PB' + PP' = s^2 BB'$$

$$B'(B+P) + P'(B+P) = s^2 BB'$$

$$P'(B+P) = s^2 BB' - B'(B+P)$$

$$P' = \frac{-B'(B+P - s^2 B)}{B+P}$$

more bio sense to $-P'$ than $-B'$

$$-\frac{dP}{dE} = \frac{dB}{dE}\left(1 - \frac{s^2 B}{B+P}\right)$$

$$\frac{d}{dE}\left[(B+P)^2 - s^2P^2\right] = 0$$

$$\cancel{2}(B+P)(B'+P') = \cancel{2}s^2PP'$$

$$BB' + BP' + PB' + PP' = s^2PP'$$

$$B'(B+P) + P'(B+P) = s^2PP'$$

$$B'(B+P) = -P'(B+P) + s^2PP'$$

$$= -P'\left(B+P - s^2P\right)$$

$$B' = \frac{-P'(B+P-s^2P)}{B+P} = -P'\left(1 - \frac{s^2P}{B+P}\right)$$

$$\boxed{\frac{dB}{dE} = -\frac{dP}{dE}\left(1 - \frac{s^2P}{B+P}\right)}$$

$$N_{t+1} = N_t B + N_t P$$

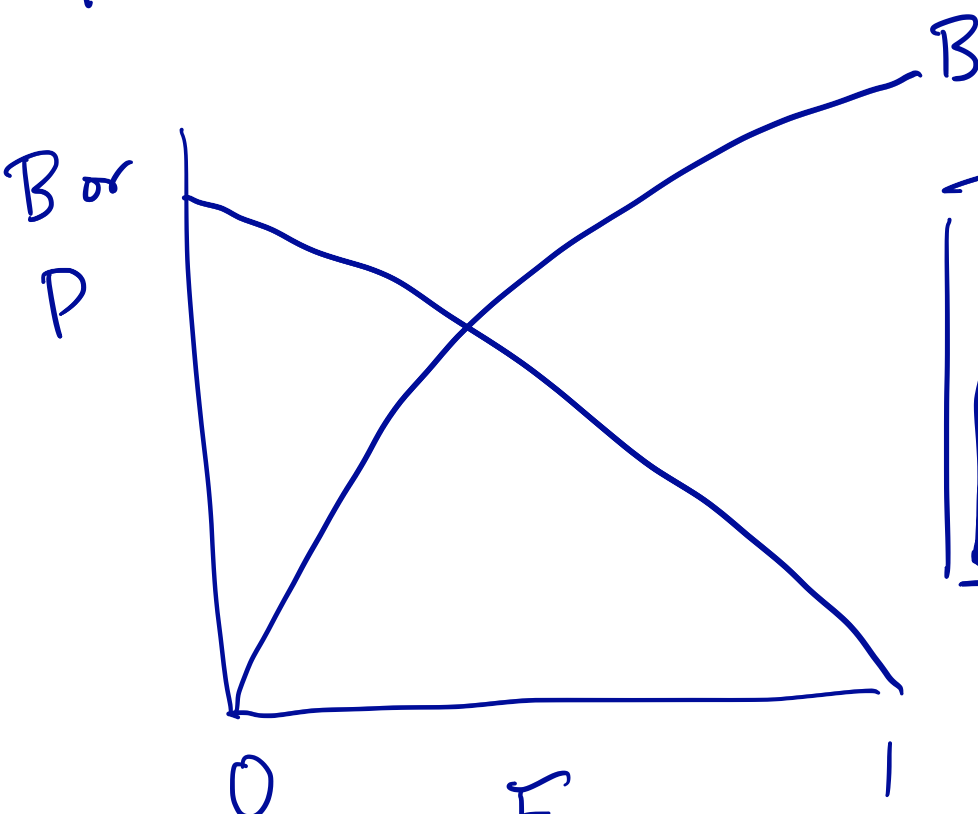
$$N_{t+1} = N_t \lambda$$

$$\boxed{\lambda = B + P}$$

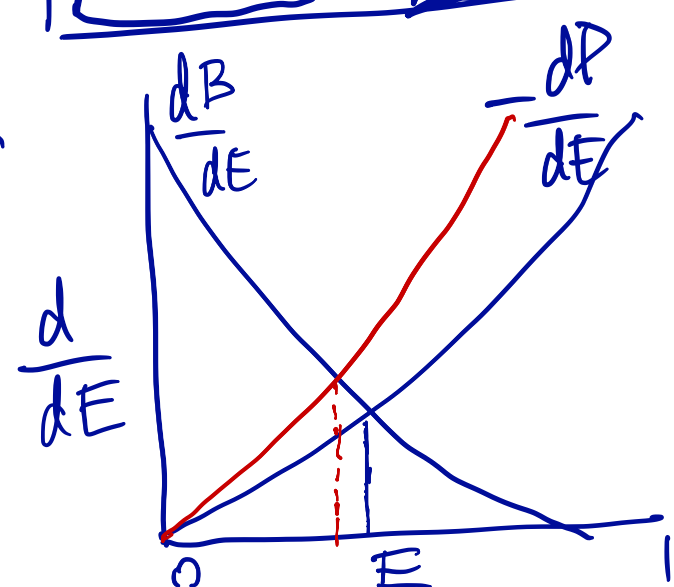
$B = B(E)$

$P = P(E)$

$$0 = \frac{d\lambda}{dE} = \frac{dB}{dE} + \frac{dP}{dE}$$



$$\boxed{\boxed{\frac{dB}{dE}} = \boxed{-\frac{dP}{dE}}}$$



Case 1 : Juvenile Survival / Fertility

$$\lambda_g = B(1+s) + P \leftarrow \quad \lambda_g \lambda_b = \bar{\lambda}^2$$

$$\lambda_b = B(1-s) + P \leftarrow$$

$$2BP + \cancel{BP}s + \cancel{BP} - \cancel{BP}s$$

$$B^2(1-s^2) + BP(1+s) + BP(1-s) + P^2 = \bar{\lambda}^2$$

$$B^2(1-s^2) + 2BP + P^2 = \bar{\lambda}^2$$

$$B^2 - B^2 s^2 + 2BP + P^2 = \bar{\lambda}^2$$

$$\boxed{(B+P)^2 - B^2 s^2 = \bar{\lambda}^2}$$

Case 2: Adult Survival

$$\lambda_g = B + (1+s)P$$

$$\lambda_b = B + (1-s)P \qquad \bar{\lambda}^2 = \lambda_g \lambda_b$$

$$\boxed{\bar{\lambda}^2 = (B+P)^2 - P^2 s^2}$$

Case 1 : Juvenile

$$\frac{d}{dE}(B+P)^2 - s^2B^2 = 0$$

$$\cancel{2}(B+P)(B'+P') - \cancel{2}s^2BB' = 0$$

$$BB' + BP' + PB' + PP' = s^2BB'$$

$$B'(B+P) + P'(B+P) = s^2BB'$$

$$P'(B+P) = s^2BB' - B'(B+P)$$

$$P' = \frac{-B'(B+P-s^2B)}{B+P}$$

$$\boxed{-\frac{dP}{dE} = \frac{dB}{dE}\left(1 - \frac{s^2B}{B+P}\right)}$$

Case 2 : Adult

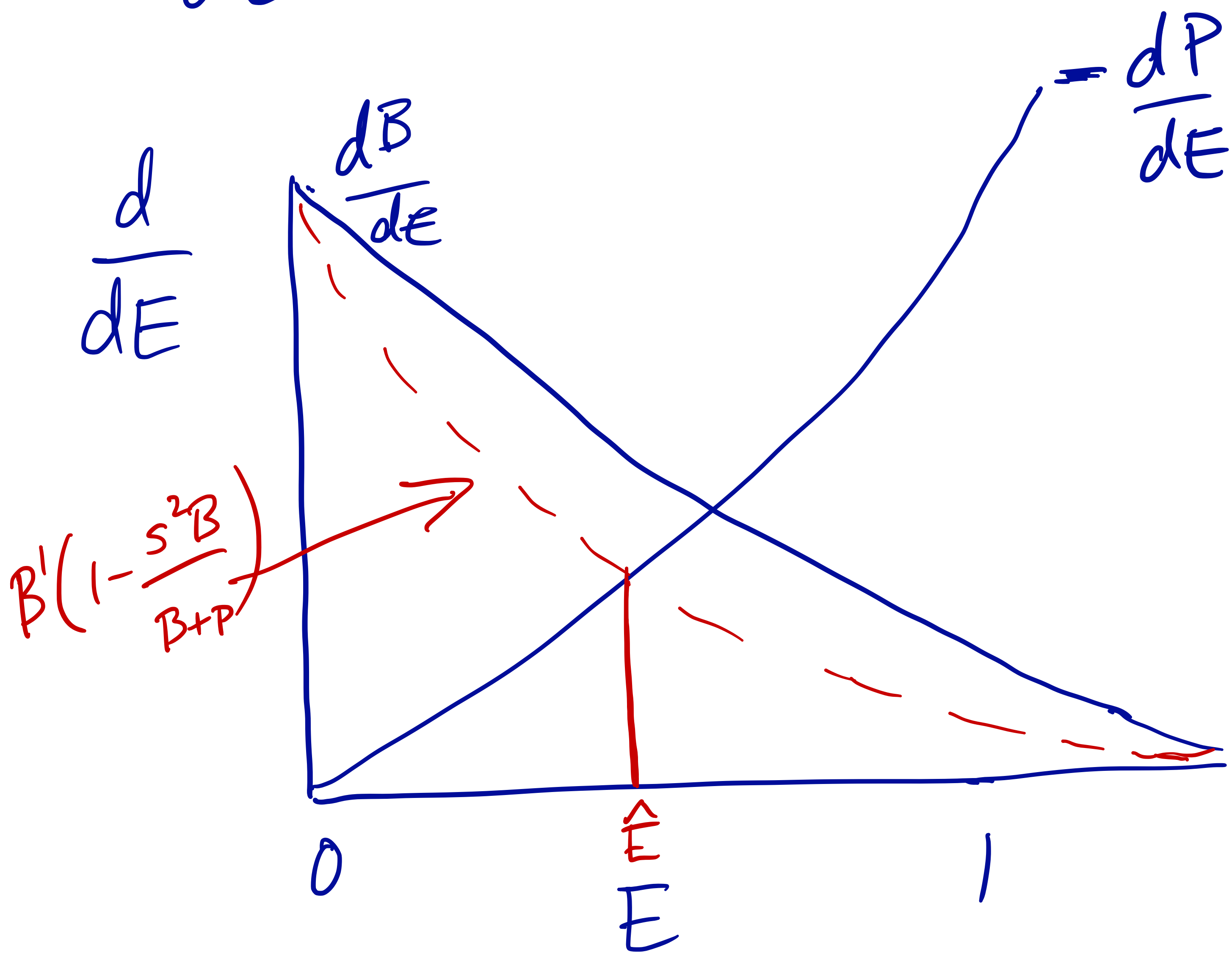
$$\frac{d}{dE}(B+P)^2 - s^2P^2 = 0$$

$\vdots$

$$\boxed{\frac{dB}{dE} = -\frac{dP}{dE}\left(1 - \frac{s^2P}{B+P}\right)}$$

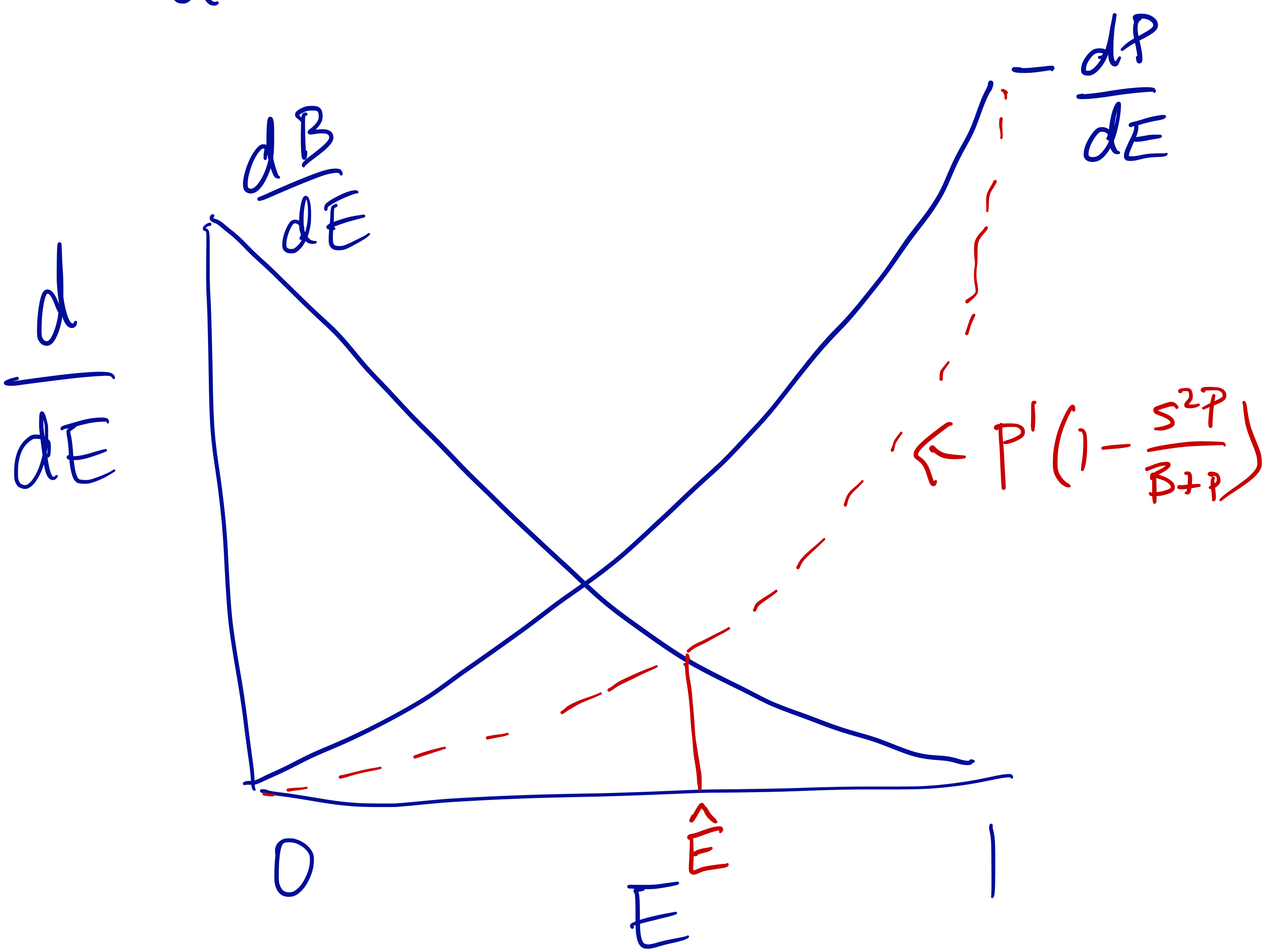
Case 1 : Juvenile Survival / Fertility

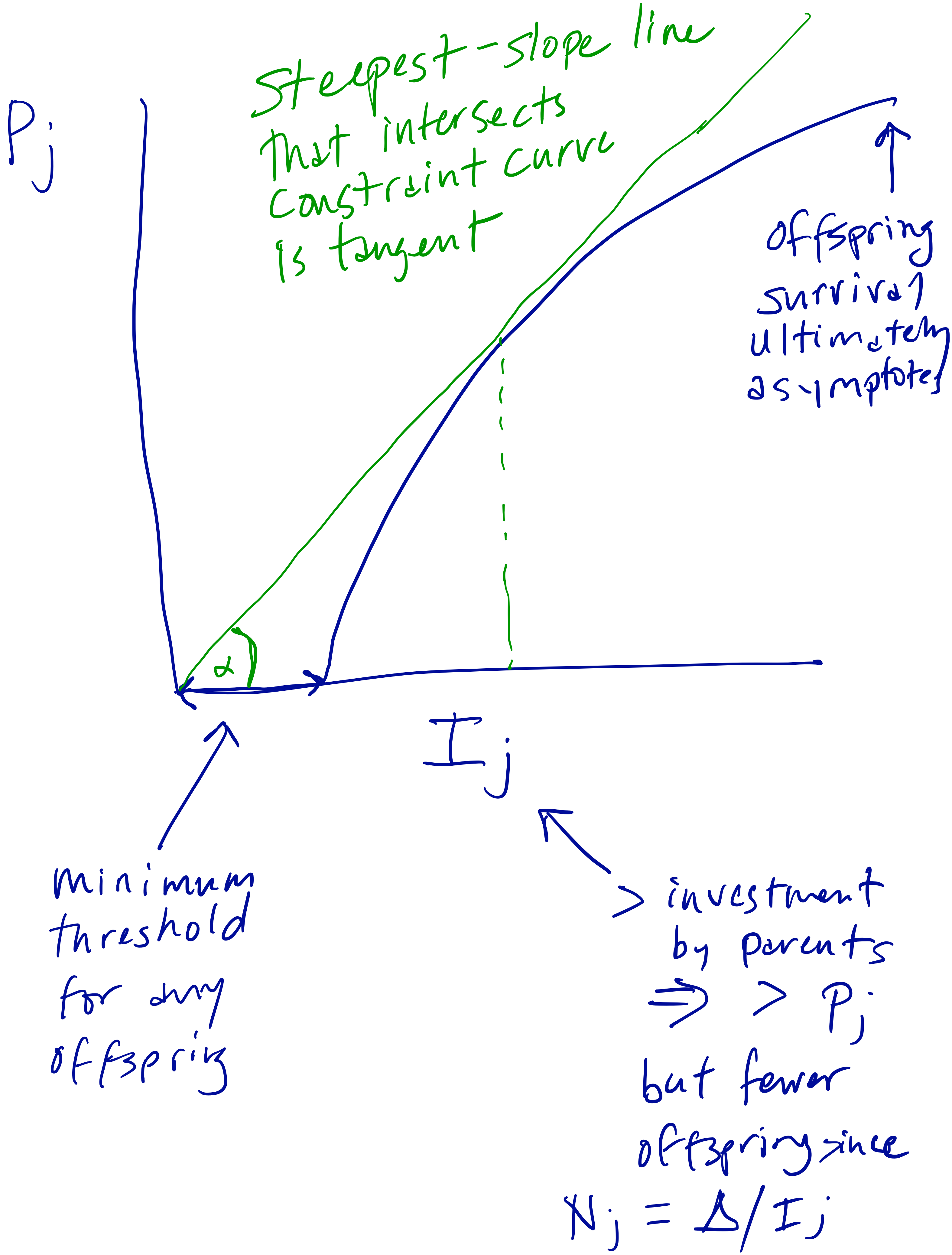
$$-\frac{dP}{dE} = \frac{dB}{dE}\left(1 - \frac{s^2 B}{B+P}\right)$$



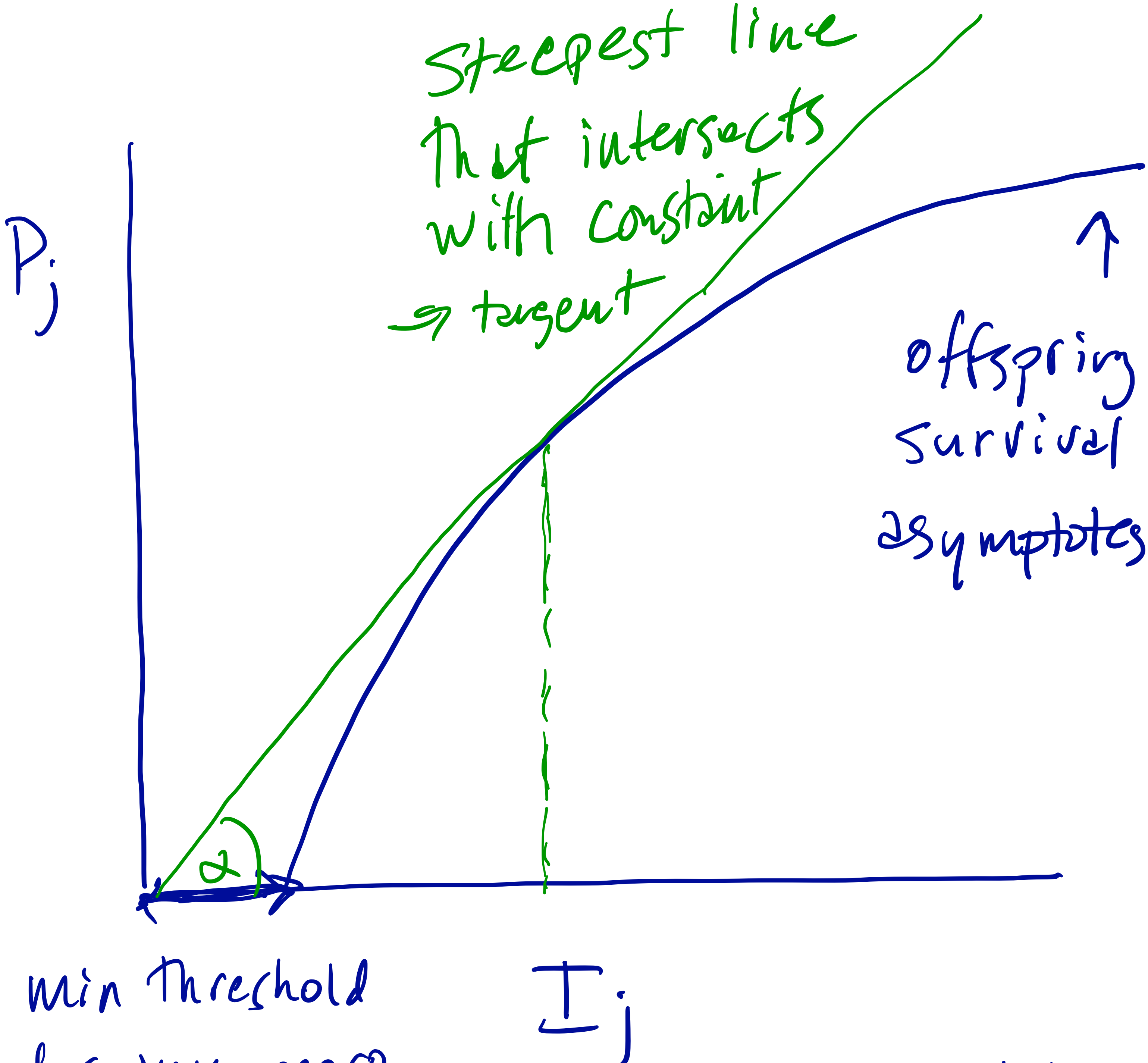
Case 2: Adult

$$\frac{dB}{dE} = -\frac{dP}{dE}\left(1 - \frac{S^2P}{B+P}\right)$$





Steepest-slope line that intersects constraint curve is tangent
P_j
α
I_j
offspring survival ultimately asymptotes
minimum threshold for any offspring
> investment by parents $\Rightarrow$ > P_j but fewer offspring since $N_j = \Delta / I_j$



$$\tan(\alpha) = \frac{\text{opposite}}{\text{adjacent}}$$

$$\boxed{N_j = \Delta / I_j}$$

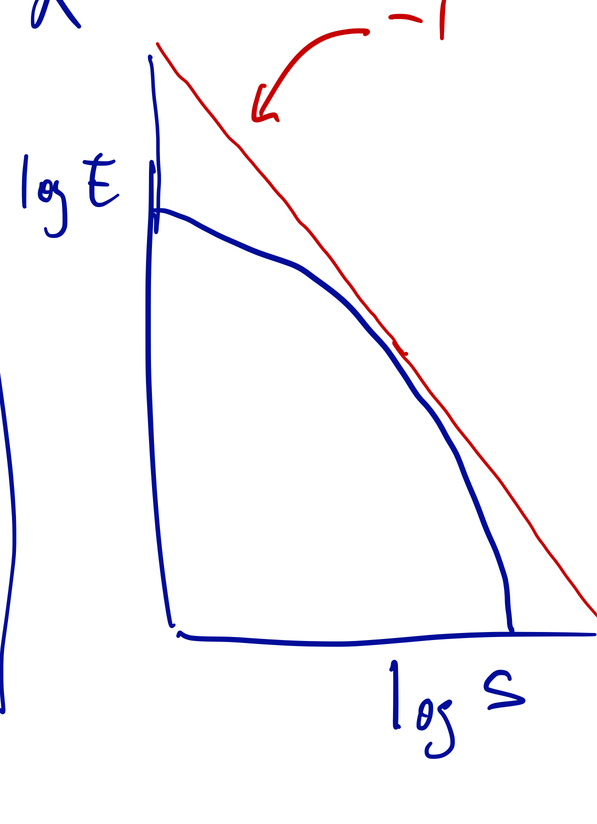
Investment by
Parents
$\Rightarrow \uparrow P_j$ <u>but</u>
fewer of them

$$\log R_0 = \log E + \log S$$

$$\frac{d \log R_0}{d\alpha} = \frac{d \log E}{d\alpha} + \frac{d \log S}{d\alpha} = 0$$

$$\frac{d \log E}{d\alpha} = -\frac{d \log S}{d\alpha}$$

$$\boxed{\frac{d \log E}{d \log S} = -1}$$



$$W_p = \frac{P_j(\theta)}{I_j(\theta)} \Delta \qquad \Delta : \text{fixed}$$

$$\frac{dW_p}{d(\theta)} = \Delta \frac{P_j' I_j - I_j' P_j}{I_j^2} = 0$$

$$P_j' I_j = I_j' P_j$$

slope of line

$$\frac{P_j}{I_j} = \frac{P_j'}{I_j'} = \frac{\frac{dP_j}{\cancel{d\theta}}}{\frac{dI_j}{\cancel{d\theta}}}$$

$$\frac{P_j}{I_j} = \frac{dP_j}{dI_j}$$

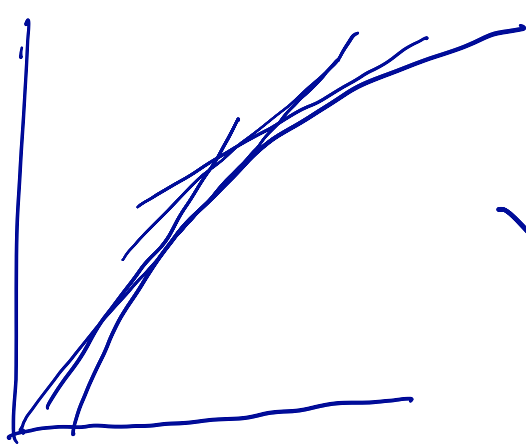
tangent of curve

$$W_p = \frac{P_j \Delta}{I_j + \delta}$$

$$\frac{dW_p}{d\theta} = \Delta \frac{P'_j (I_j + \delta) - I'_j P_j}{(I_j + \delta)^2} = 0$$

$$P'_j (I_j + \delta) = I'_j P_j$$

$$\frac{dP_j}{dI_j} = \frac{P'_j}{I'_j} = \frac{P_j}{I_j + \delta}$$



$$y = mx + b$$

$$b = y - mx'$$

$$= m \cdot x - mx$$

$$5x - dx = 0$$

Taylor Series of $\log(\lambda)$

– perform expansion around $\bar{\lambda}$

$f = \log(\lambda)$ $\quad f'' = -1/\lambda^2$

$f' = 1/\lambda$

$$\log(\lambda) = \underbrace{\log(\bar{\lambda})}_{\mathbb{E}(\cdot) = \log(\bar{\lambda})} + \frac{1}{\lambda}\underbrace{(\lambda - \bar{\lambda})}_{\mathbb{E}(\cdot) = 0} + $$

$$- \frac{1}{\lambda^2}\frac{1}{2}\underbrace{(\lambda - \bar{\lambda})^2}_{\mathbb{E}(\cdot) = \sigma^2} + \cdots$$

Take Expectations!

$$\boxed{\mathbb{E}(\log(\lambda)) = \log(\bar{\lambda}) - \boxed{\frac{\sigma^2}{2\bar{\lambda}}}}$$

$$\frac{dW}{dt} = A W^{0.75}$$

Annual fertility

$$\boxed{\boxed{\frac{d}{d\alpha}\log\frac{dW}{dt}} = \boxed{\frac{d\log b}{d\alpha}}}$$

AFR

$$\log\left(\frac{dW}{dt}\right) = \log A + 0.75\log W$$

$$\frac{d}{d\alpha}\log\left(\frac{dW}{dt}\right) = \boxed{\frac{0.75\, W'(\alpha)}{W(\alpha)}}$$

$$= n$$

$$\boxed{\frac{d \log b}{d\alpha} = M}$$

adult instantaneous mortality rate

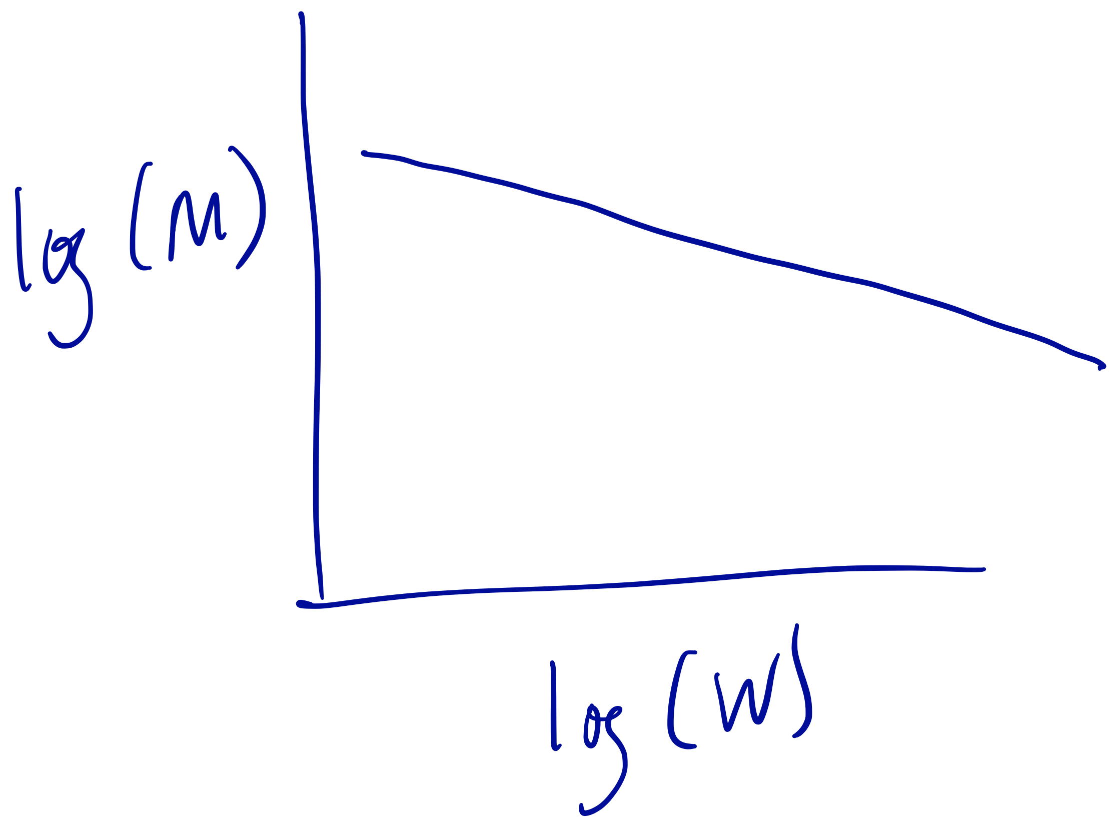
$$E = \frac{1}{M}$$

adult life expectancy

$$\frac{0.75\, W'(\alpha)}{W} = M$$

$$\frac{0.75\, A W^{0.75}}{W} = M$$

$$\boxed{M = 0.75\, W(\alpha)^{-0.25}}$$



$$R_0 = \int_0^\infty l(x)\, m(x)\, dx$$

$$= l(\alpha) \underbrace{\left[\frac{\int_\alpha^\infty l(x)\, m(x)\, dx}{l(\alpha)} \right]}_{V(\alpha)}$$

$m(x) = b \quad \forall\ x$

$$R_0 = l(\alpha)\, b \underbrace{\int_\alpha^\infty l(x)\, dx \,/\, l(\alpha)}_{E}$$

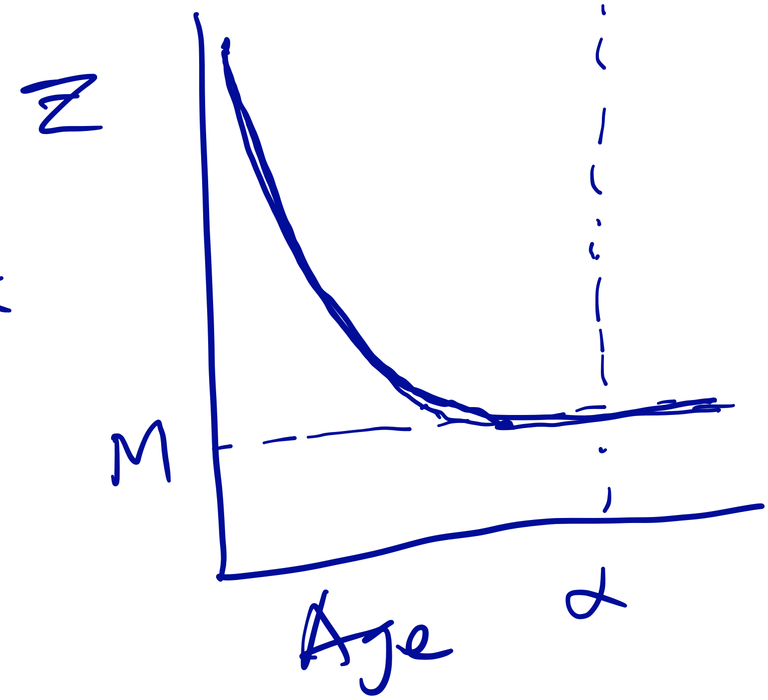
$$\boxed{R_0 = l(\alpha)\, b\, E} = l(\alpha)\, V(\alpha)$$

$$R_0 = l(\alpha)\, b\, E$$

$$l(\alpha) = e^{-\int_0^{\alpha} Z(x)\,dx}$$

$$\log l(\alpha) = -\int_0^{\alpha} Z(x)\,dx$$

$$\frac{d \log l(\alpha)}{d\alpha} = -Z(\alpha)$$



$$\log R_0 = \log l(\alpha) + \log b + \log E$$

$$\frac{d \log R_0}{d\alpha} = \frac{d \log l(\alpha)}{d\alpha} + \frac{d \log b}{d\alpha} + \frac{d \log E}{d\alpha}$$

$$= -Z(\alpha) + \frac{d \log b}{d\alpha} + 0$$

$$\frac{d \log R_0}{d\alpha} = -Z(\alpha) + \frac{d \log b}{d\alpha} = 0$$

$$\boxed{\frac{d \log b}{d\alpha} = Z(\alpha) = M}$$