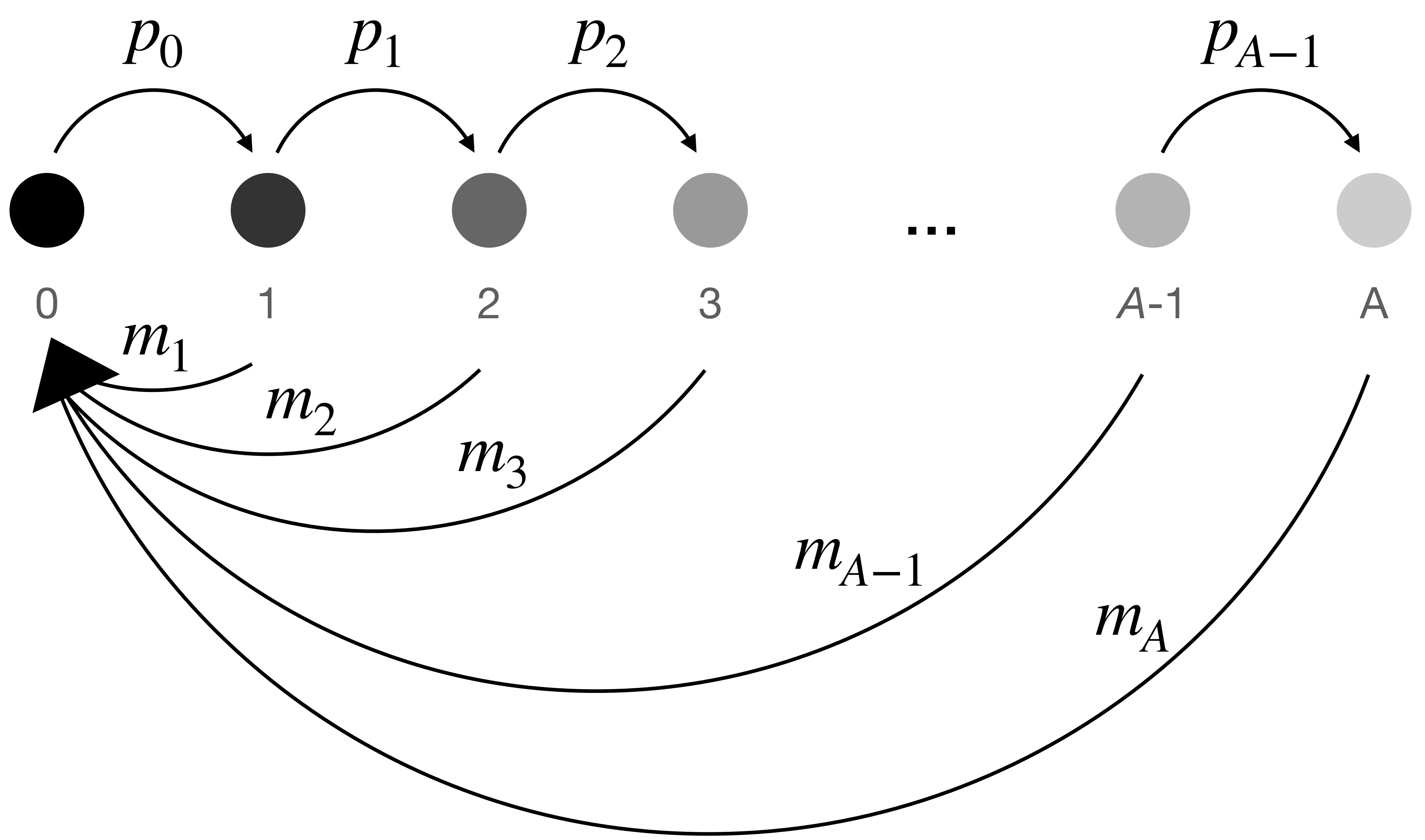
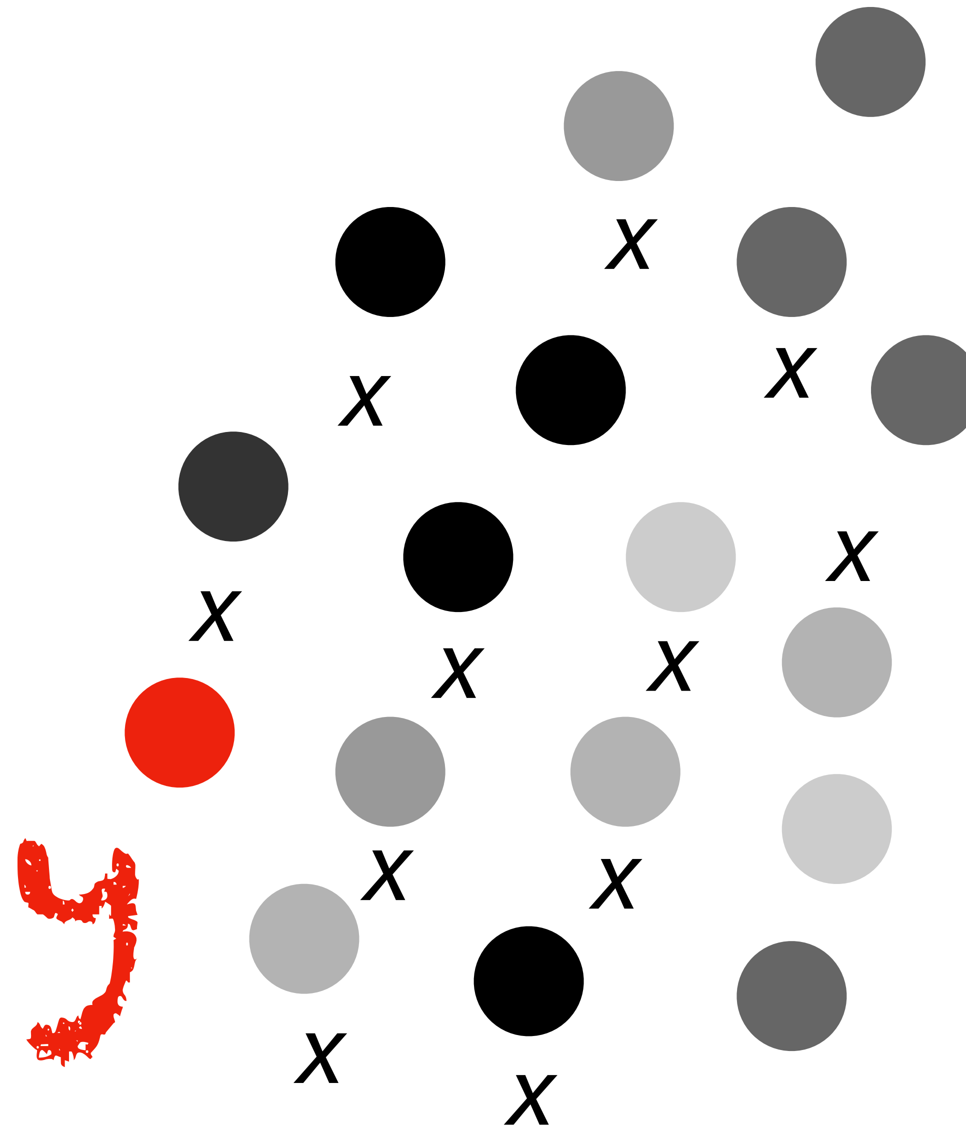
Quick recap



- Dynamics of age structured population modelled via the Leslie matrix.
- The population grows when lifetime reproductive success R_0 is above 1.
- Due to competition, natural populations eventually experience density-dependent competition.
- Populations thus stabilise to a demographic equilibrium where $R_0 = 1$.
- A rare mutant y invades an x population at demographic equilibrium when mutant reproductive success $R_0(y, x) > 1$.

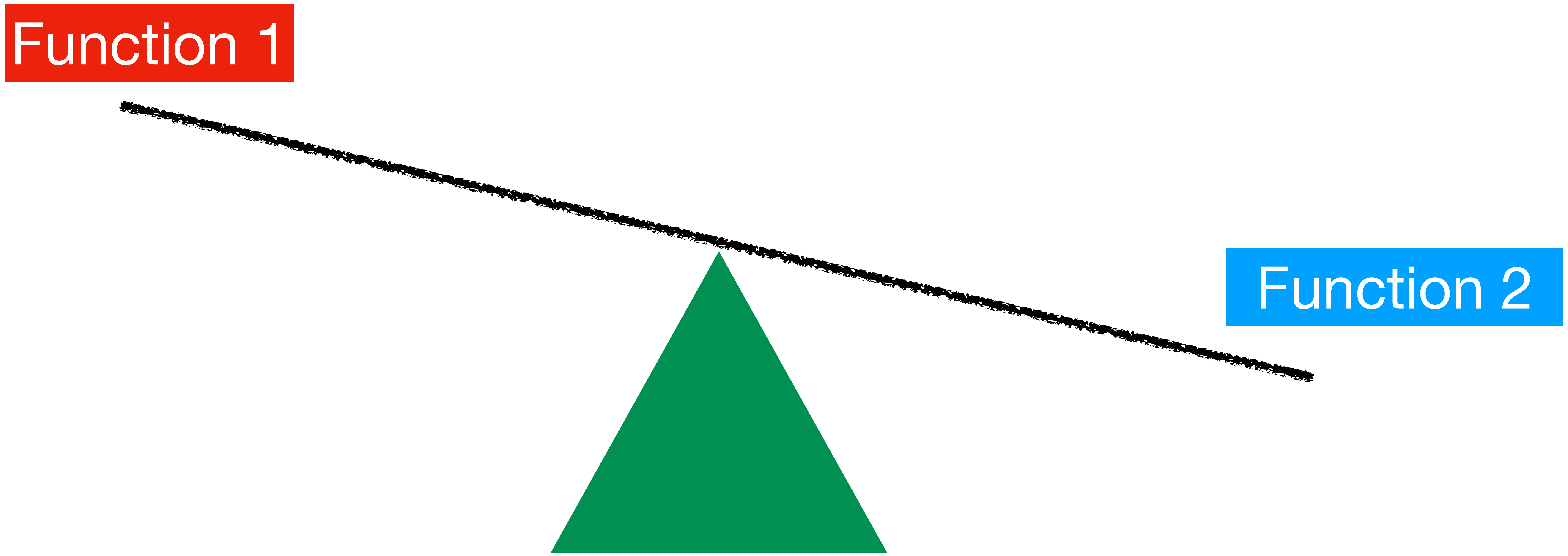
$$R_0 = \sum_{a=1}^{A} l_a m_a$$



Life-history evolution

Trade offs

due to finite resources



Example

Fecundity *vs.* offspring survival

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- Individuals live one year and reproduce once.

- Females have access to same amount of resources. They invest share x into fecundity and 1-x into parental care that improves survival from age 0 to 1.

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$$m_1(y, x) = cy$$

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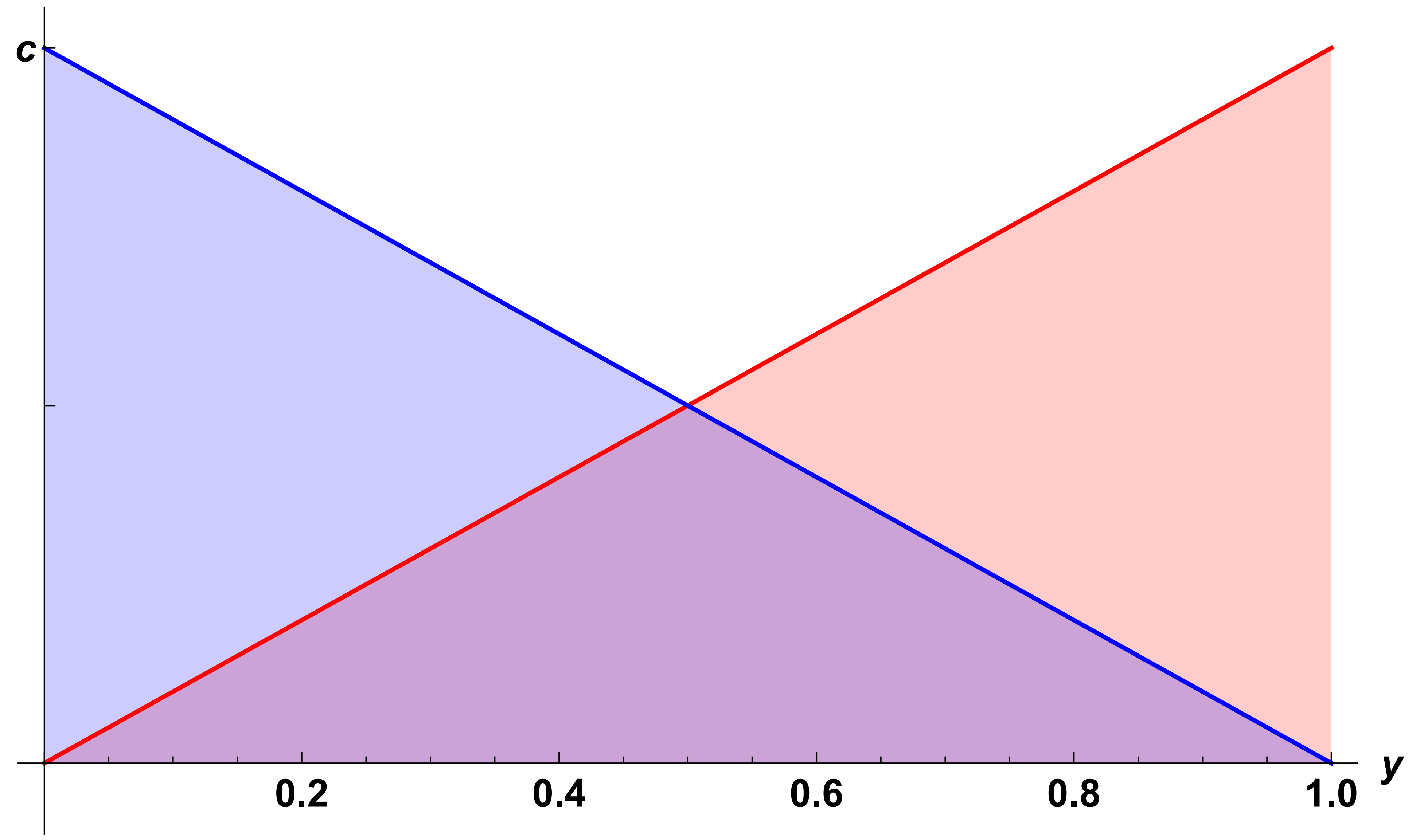
$$p_0(y, x) = (1 - y)K(x)$$

$K(x) > 0$
Density-dependent competition from resident



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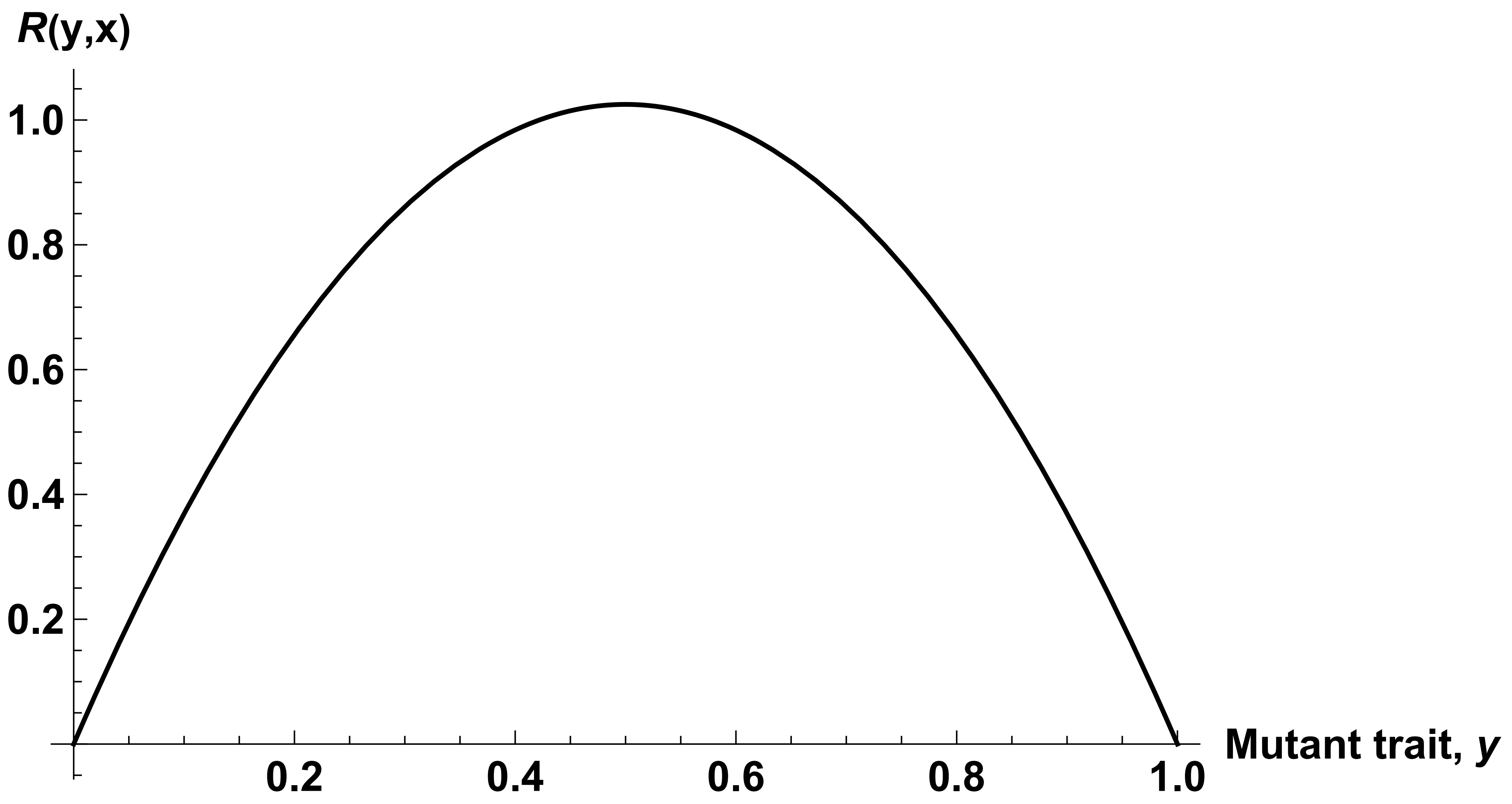

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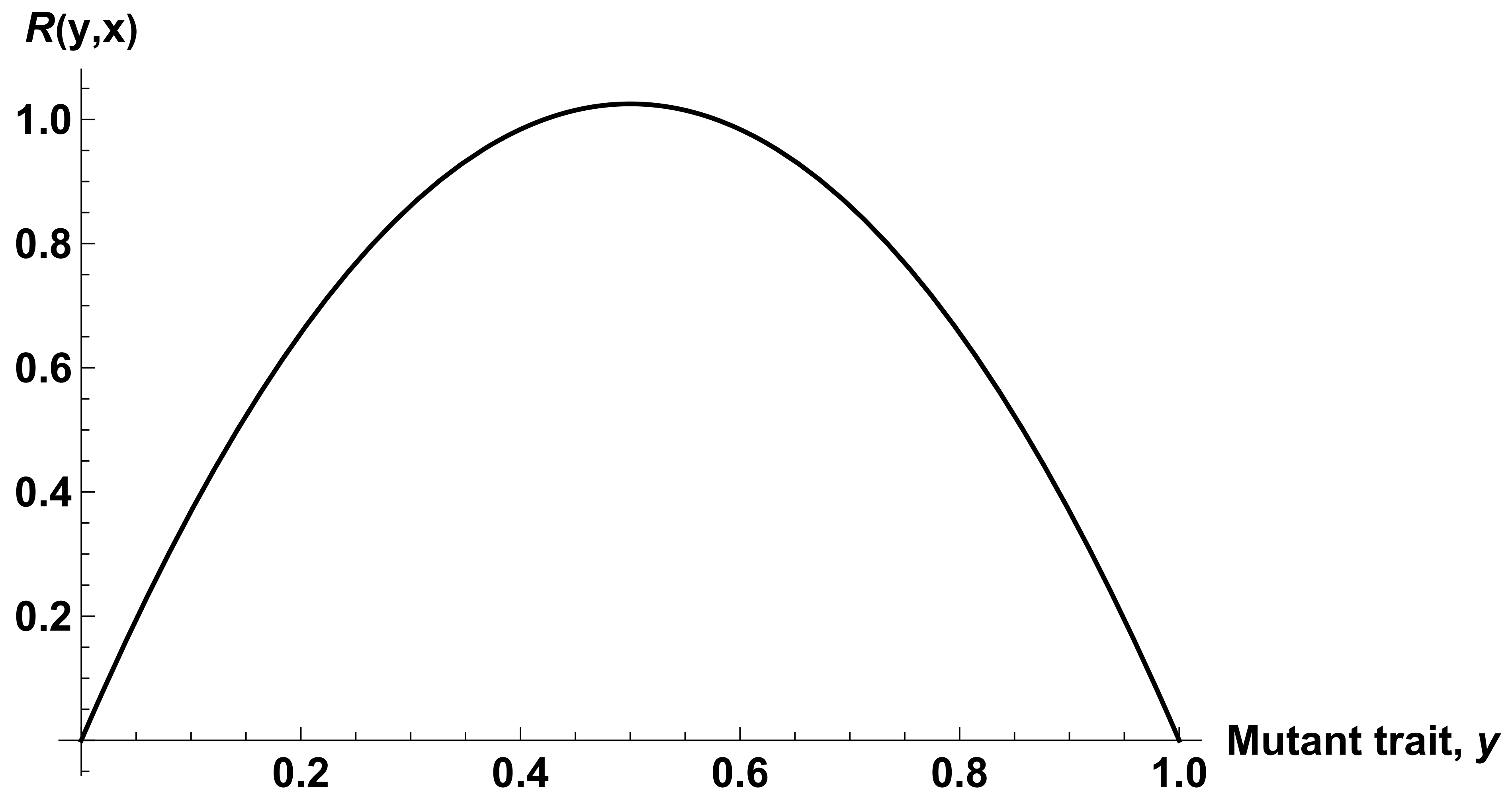

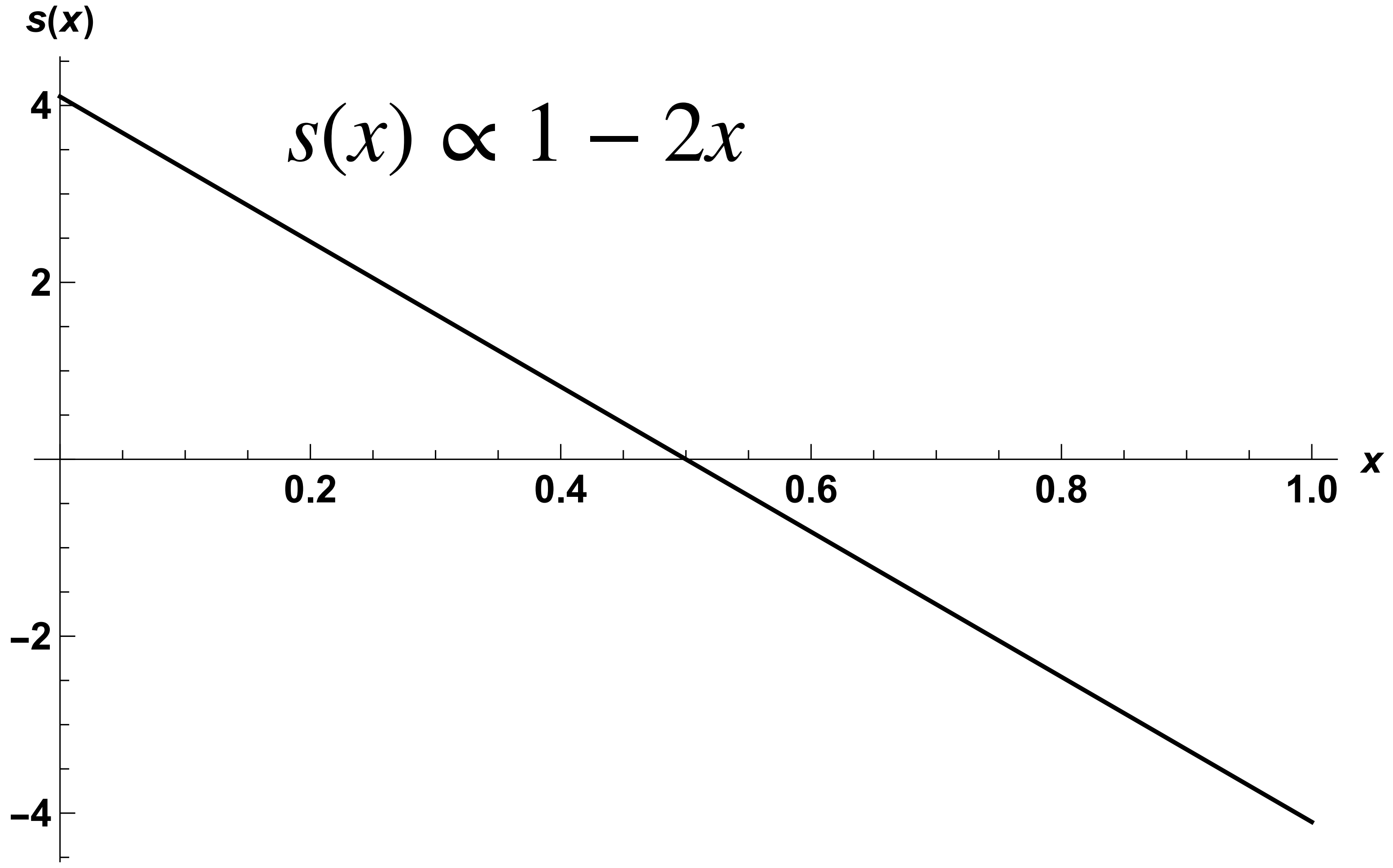

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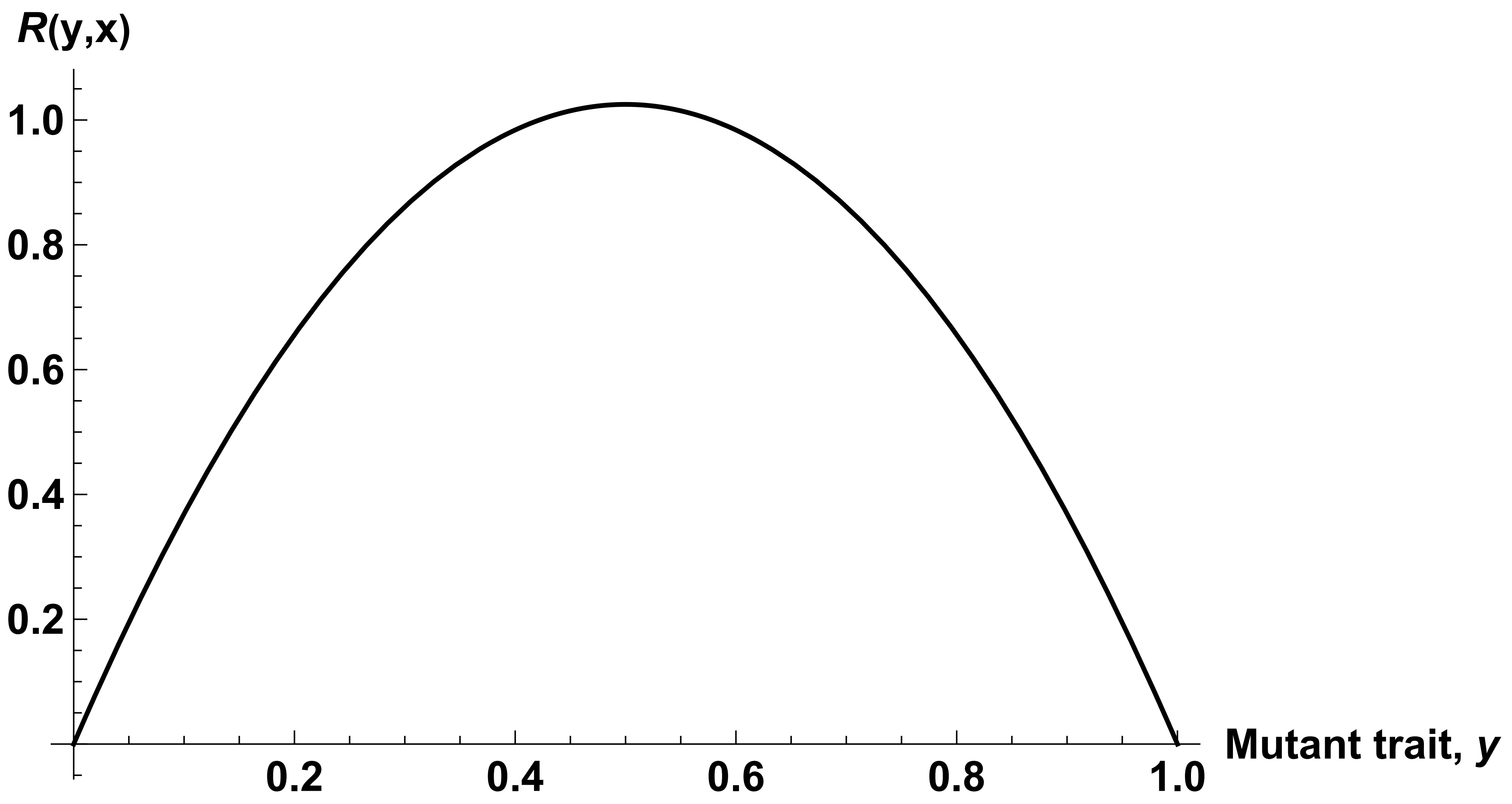
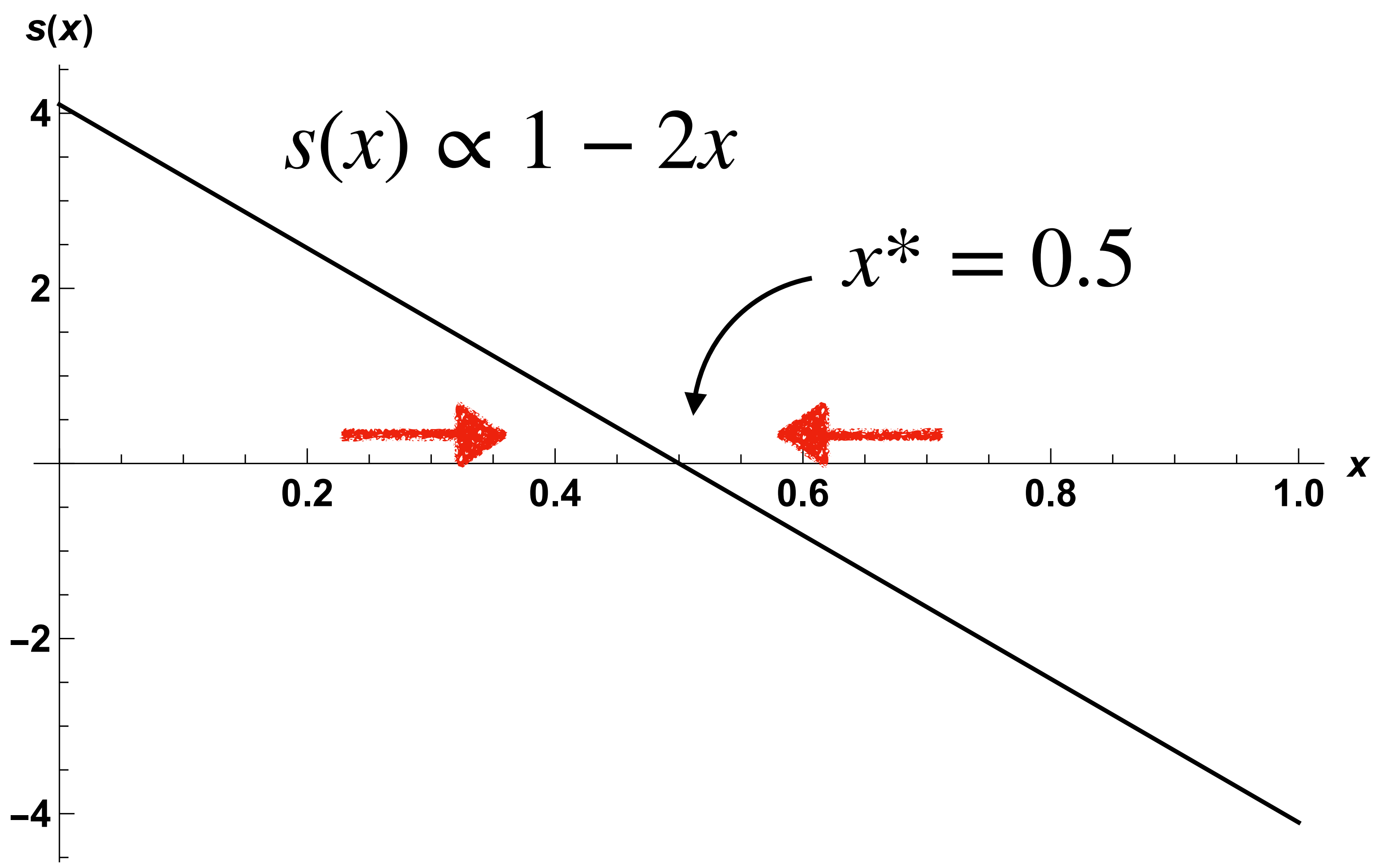




Iteroparity *vs.* semelparity

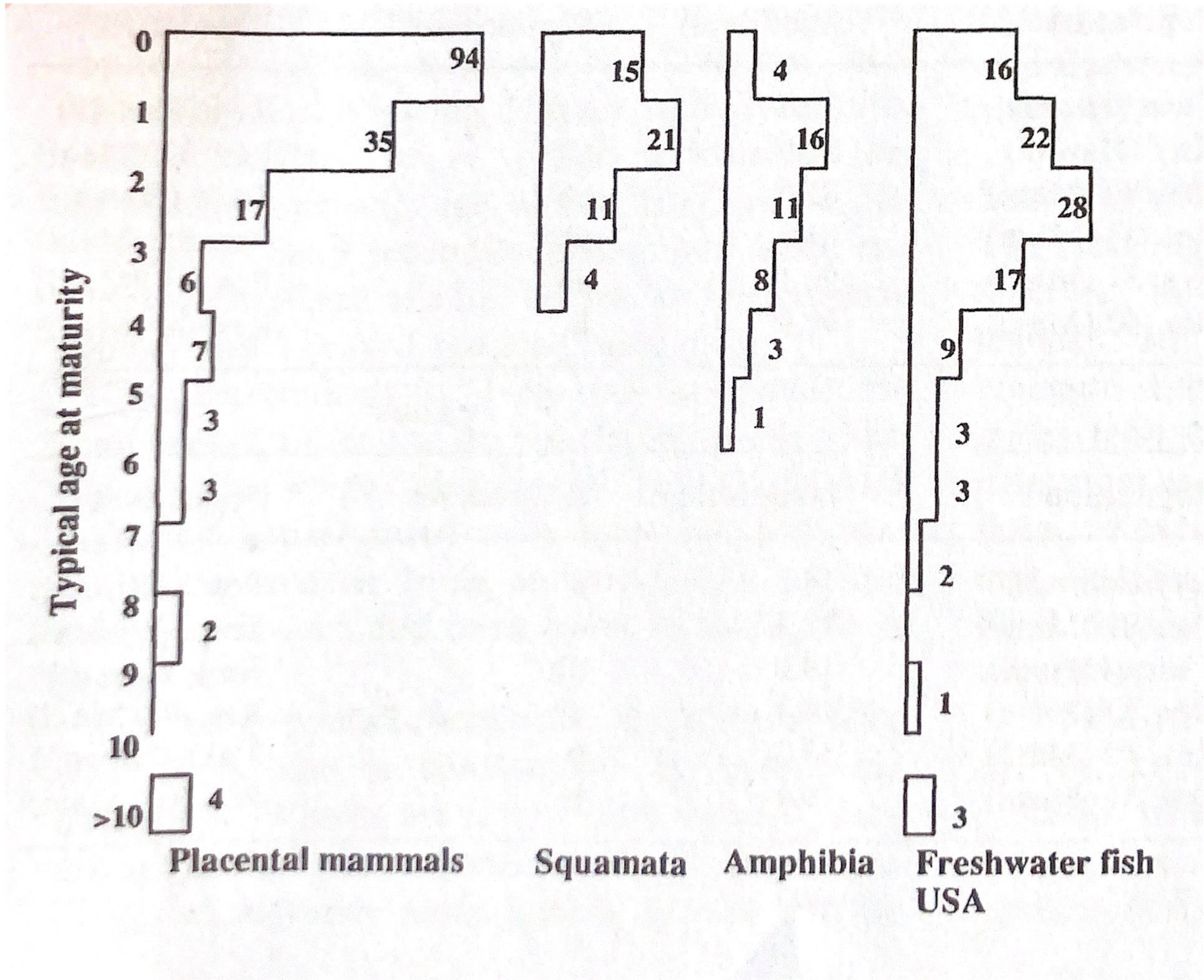
Exercise sheet - Trade off between adult survival and fecundity

- **Semelparity**: Reproduce only once during one's lifetime

- **Iteroparity**: Reproduce multiple times

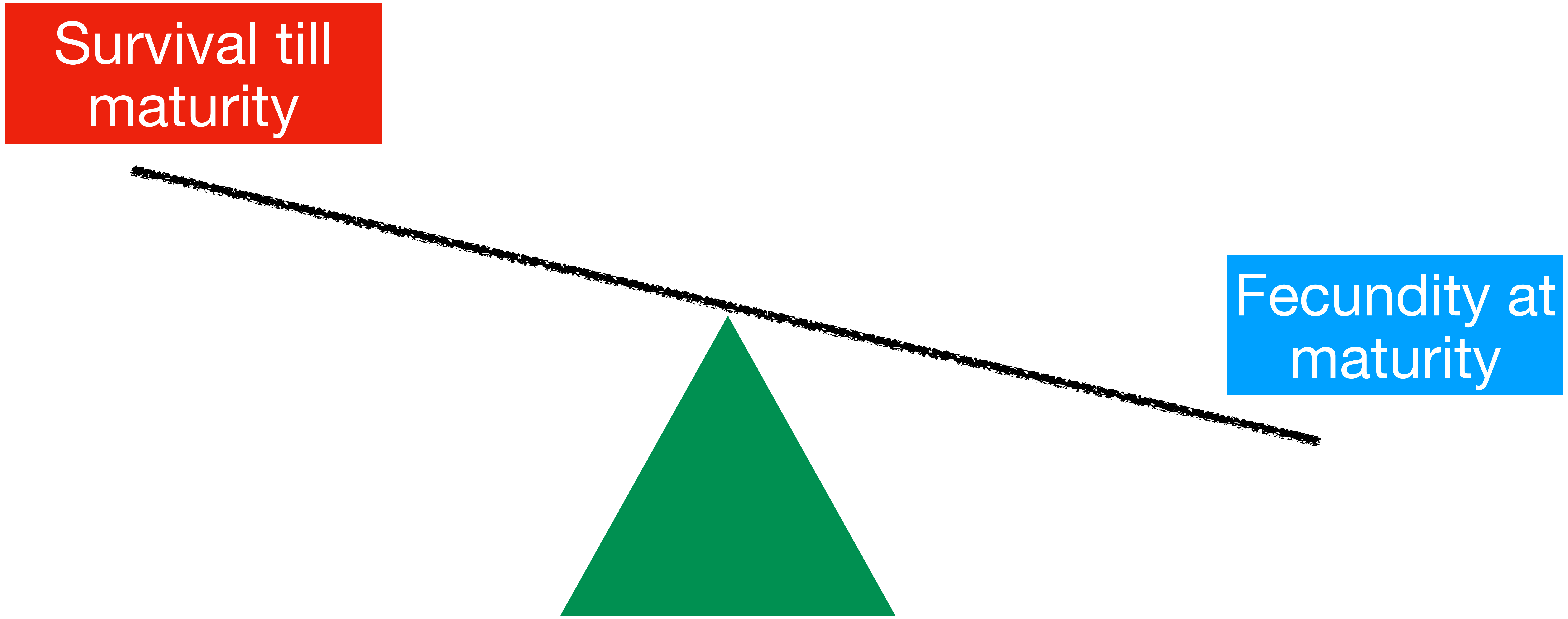
Age at maturity

- Age at which a juvenile body matures to become capable of sexual reproduction



Bell (1980) Am Nat
Stearns (1992)

Age at maturity



Age at maturity
A model

- Age at maturity, *y*, evolving trait:

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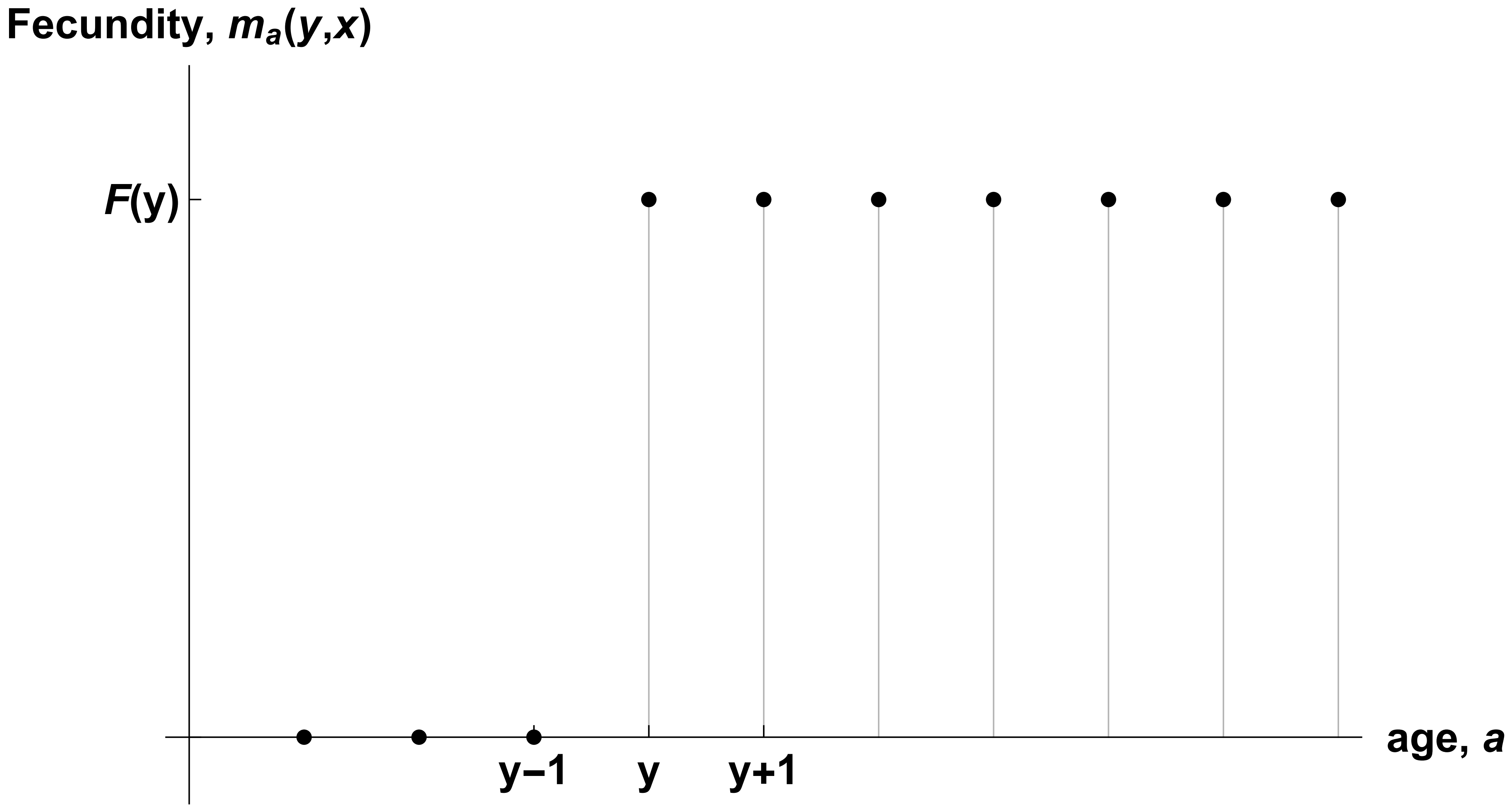
where fecundity increases with age at maturity, $F(y)$.



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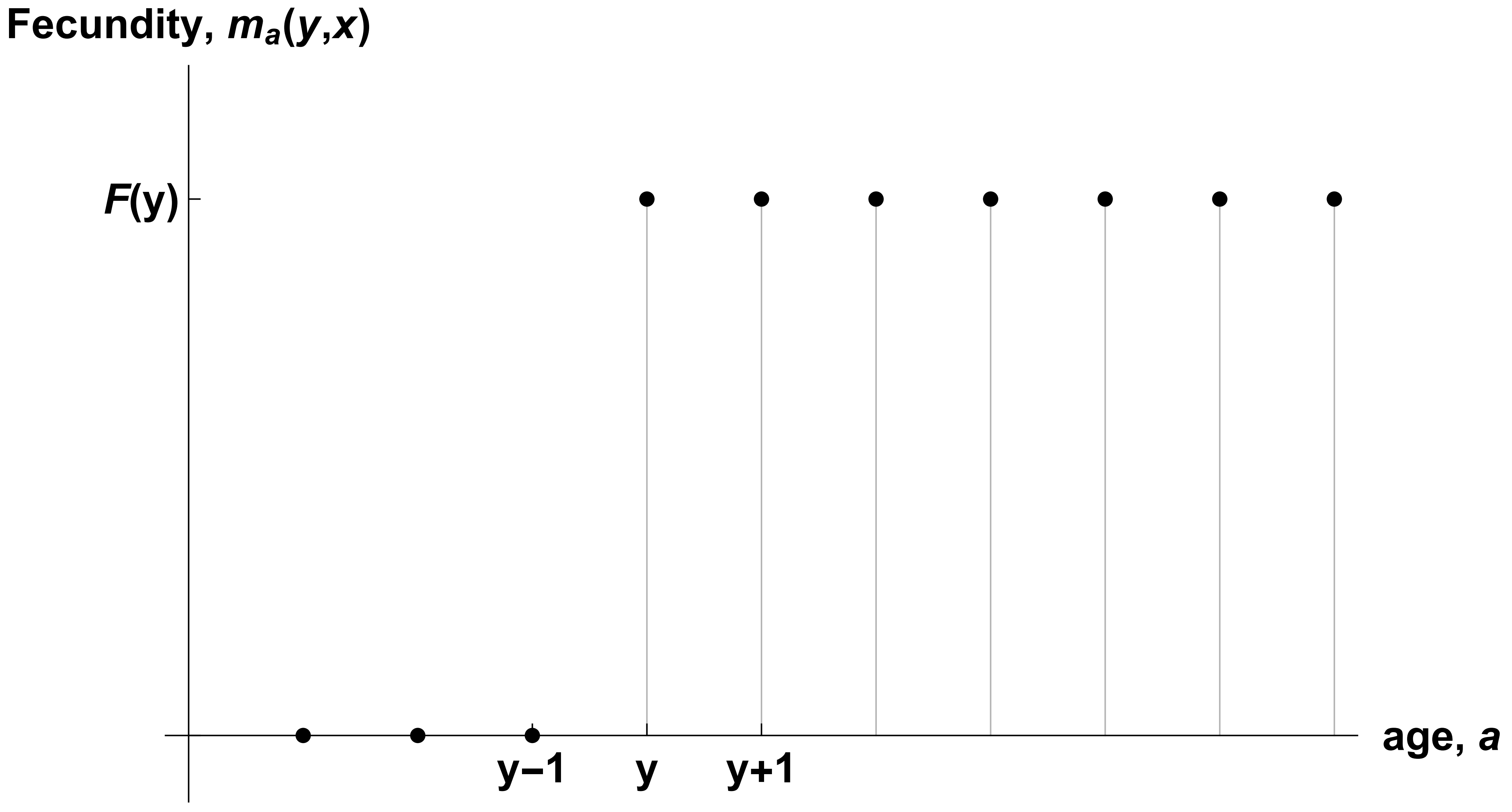

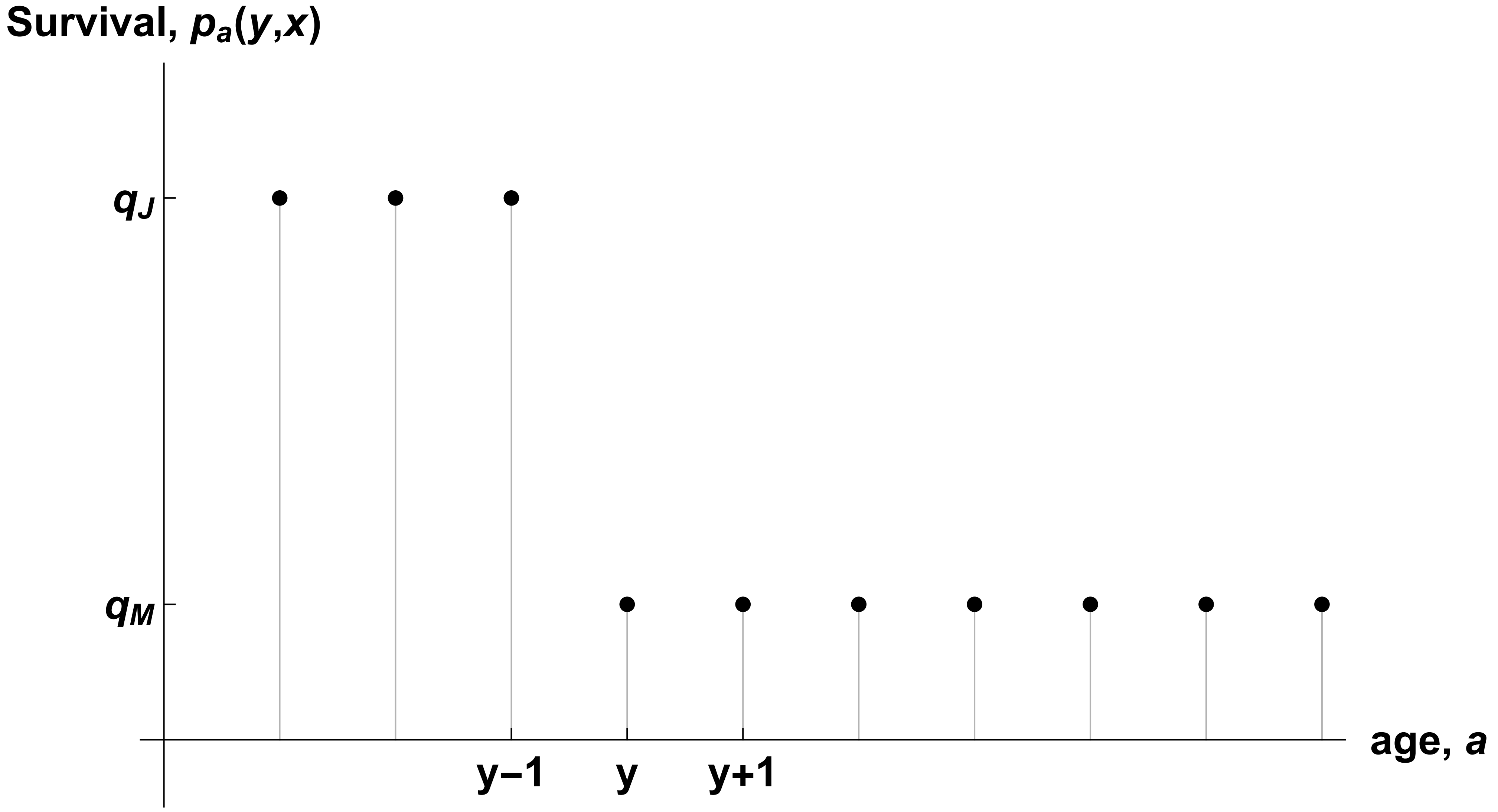

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When is it advantageous to delay maturity by a year?

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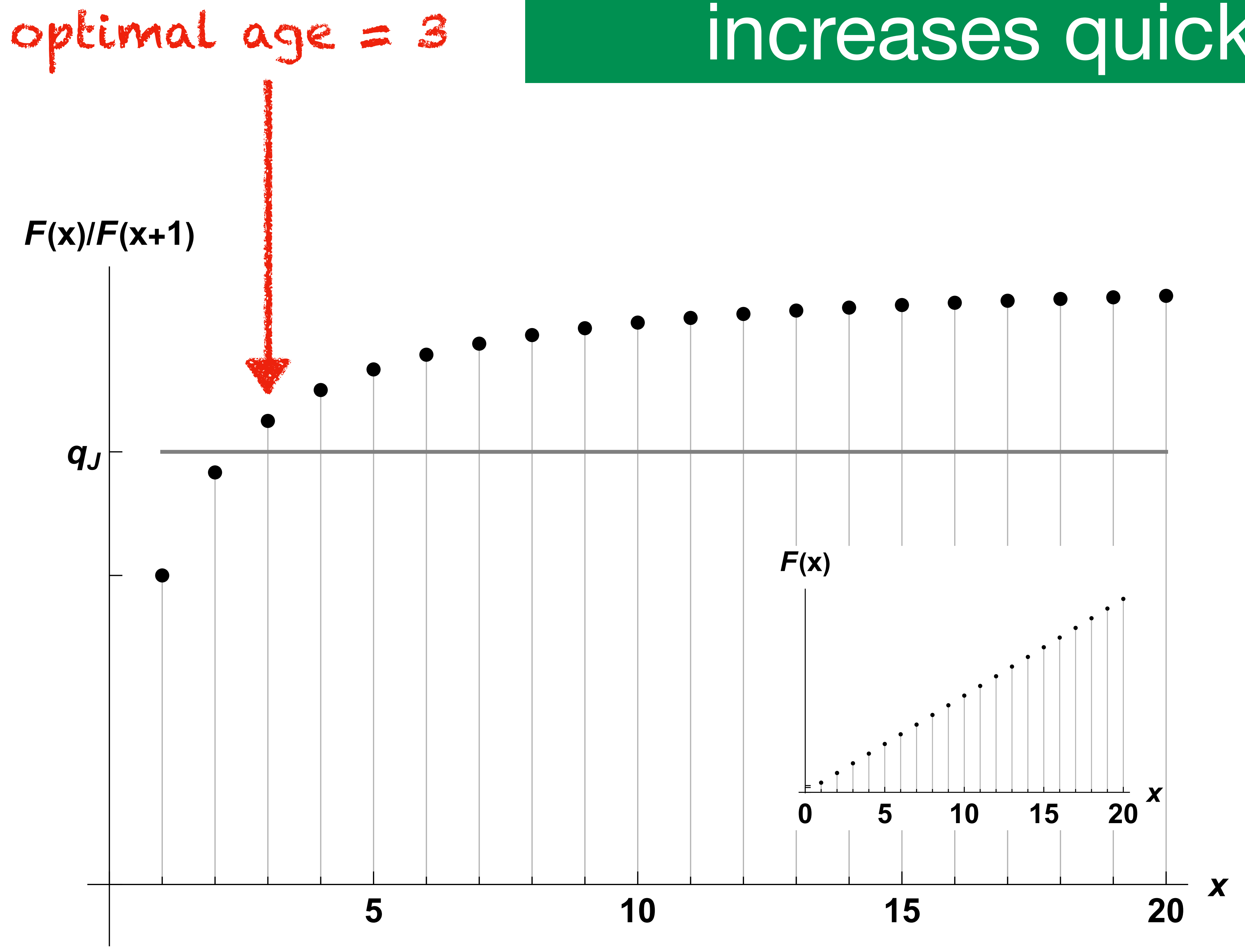

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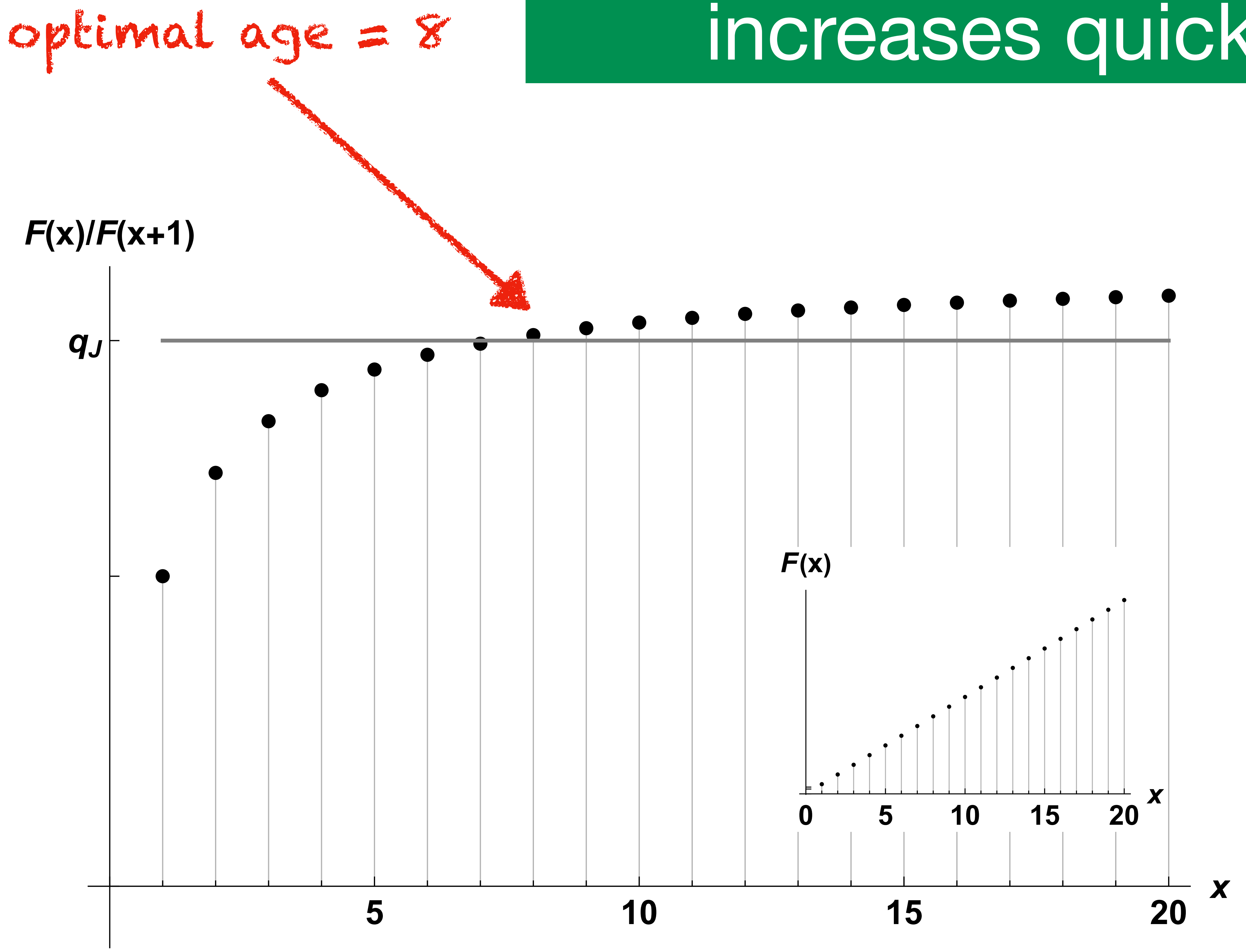

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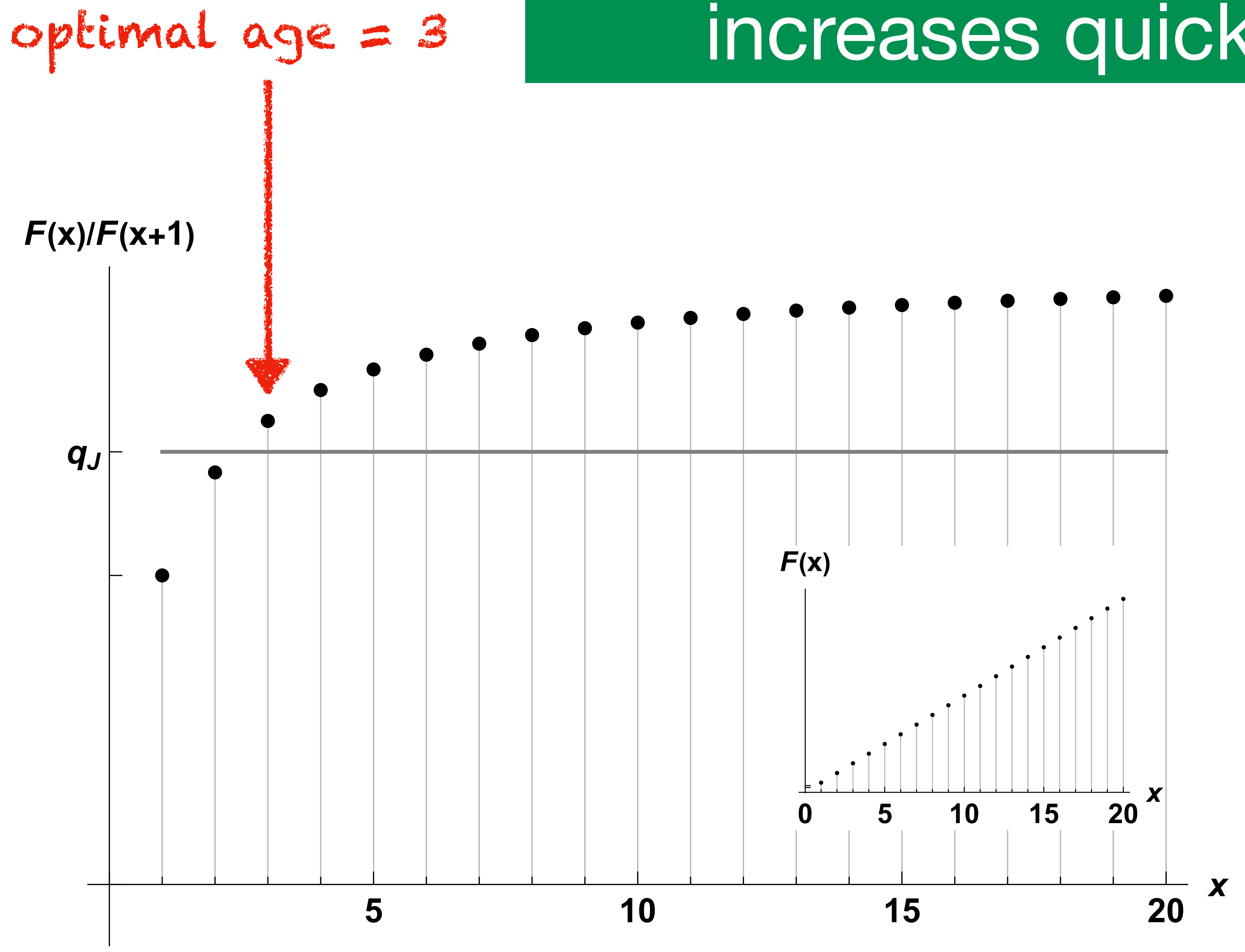

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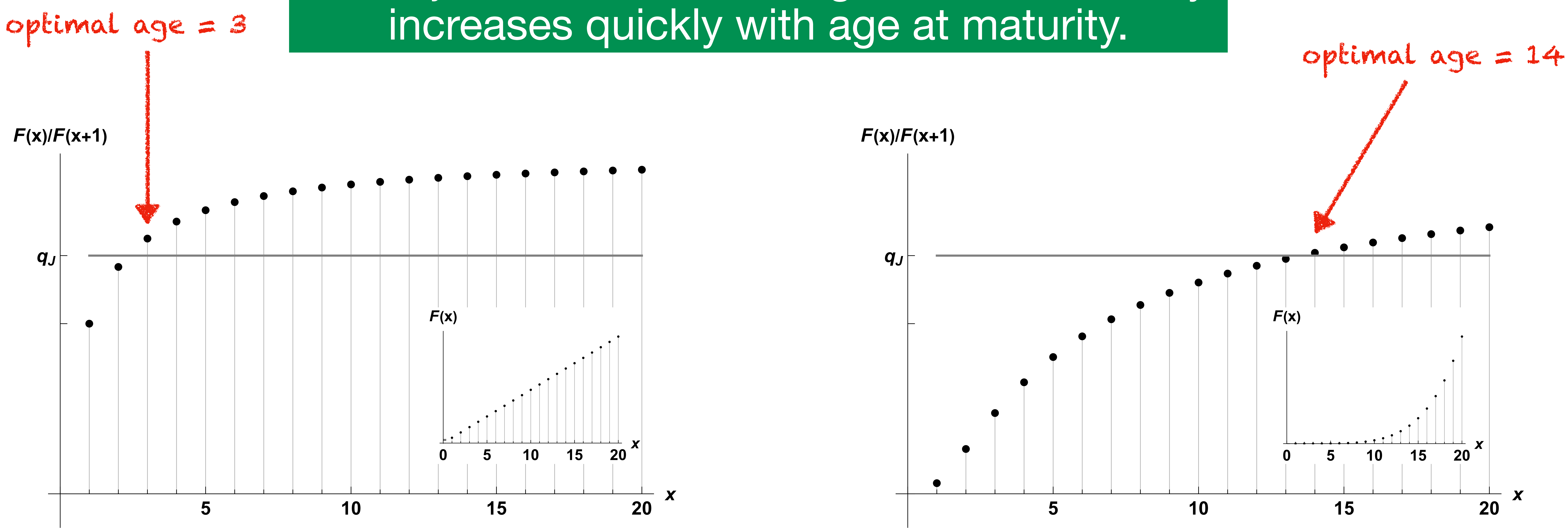
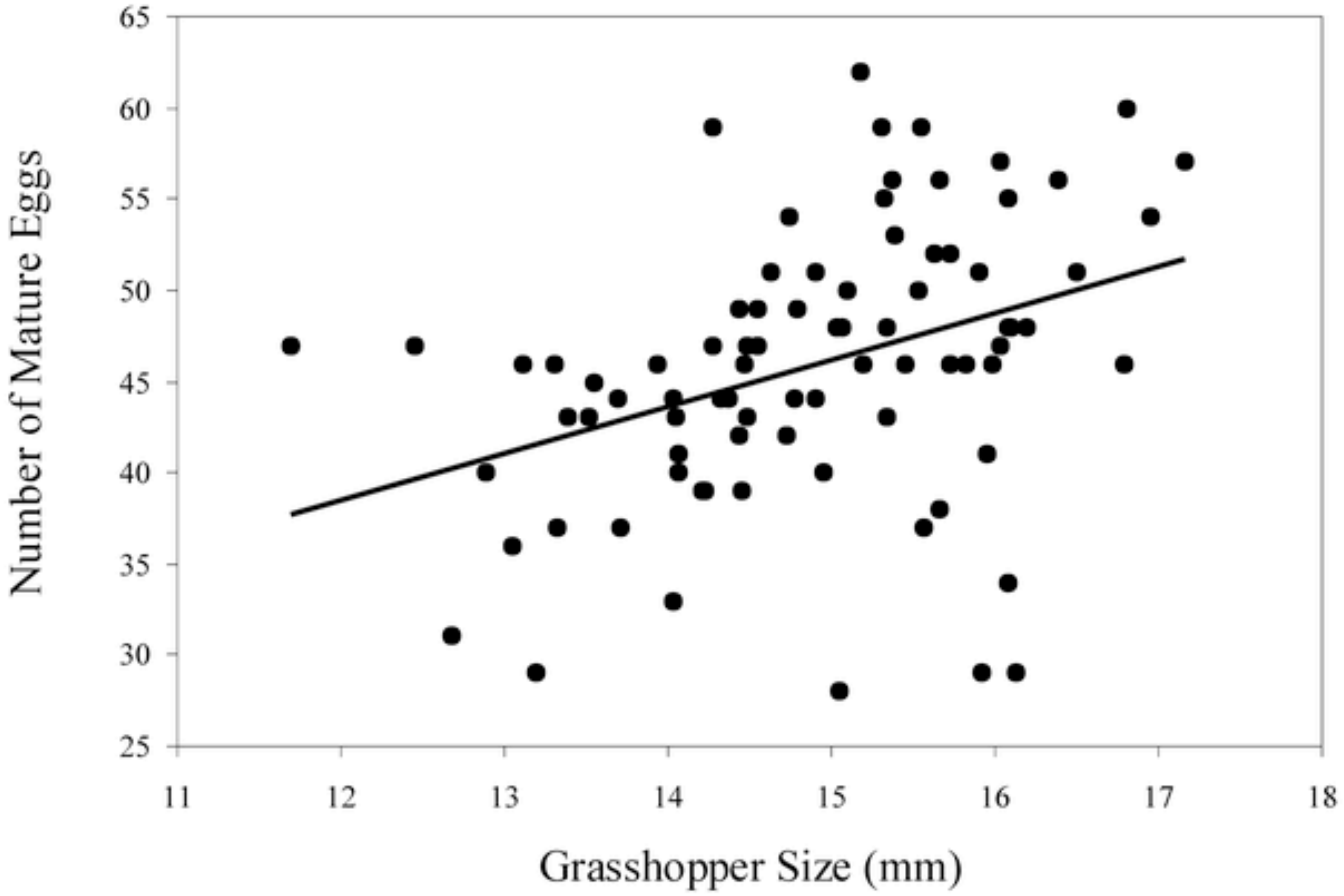


Effect of size at maturity

Fecundity associated with size in many species



J. of Orthoptera Research, 17(2):265-271 (2008)

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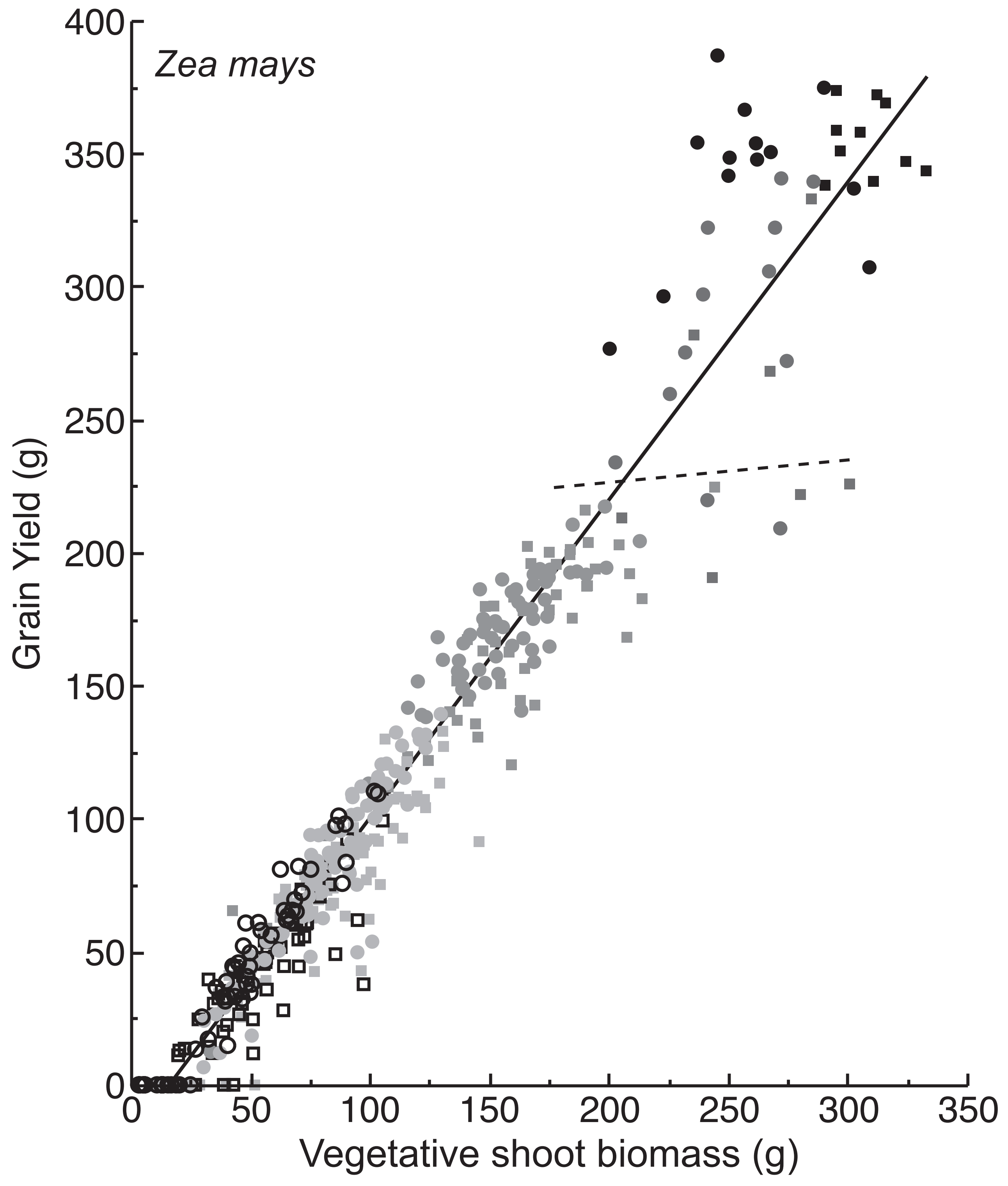
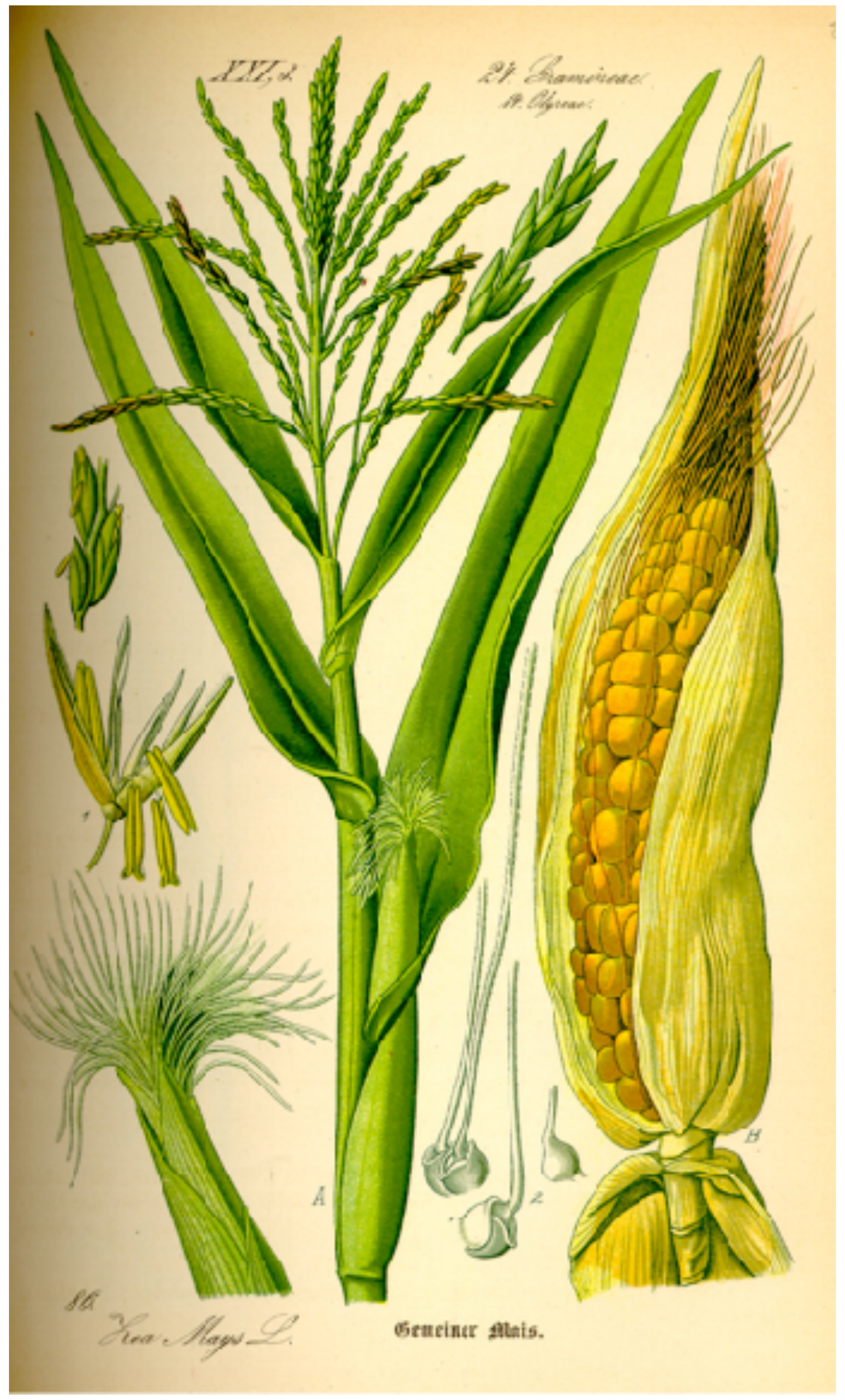
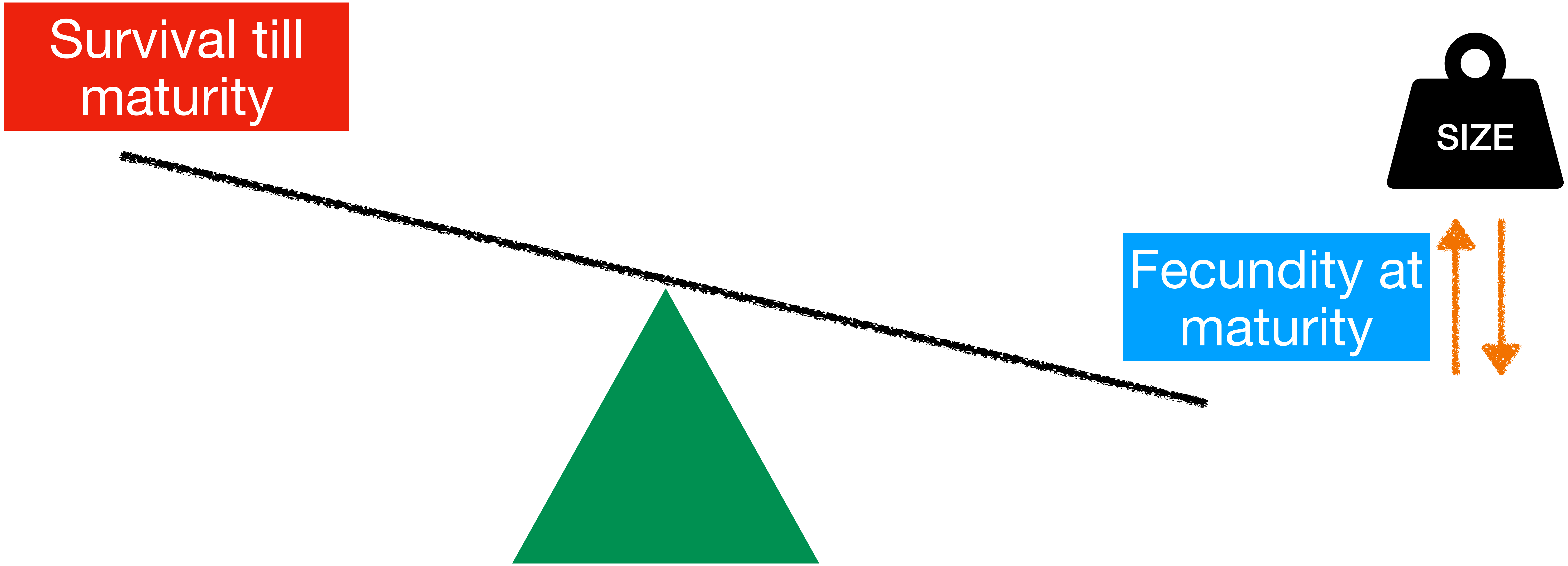


Weiner et al. Journal of Ecology 2009



Effect of size at maturity

Mediates the survival/fecundity trade-off

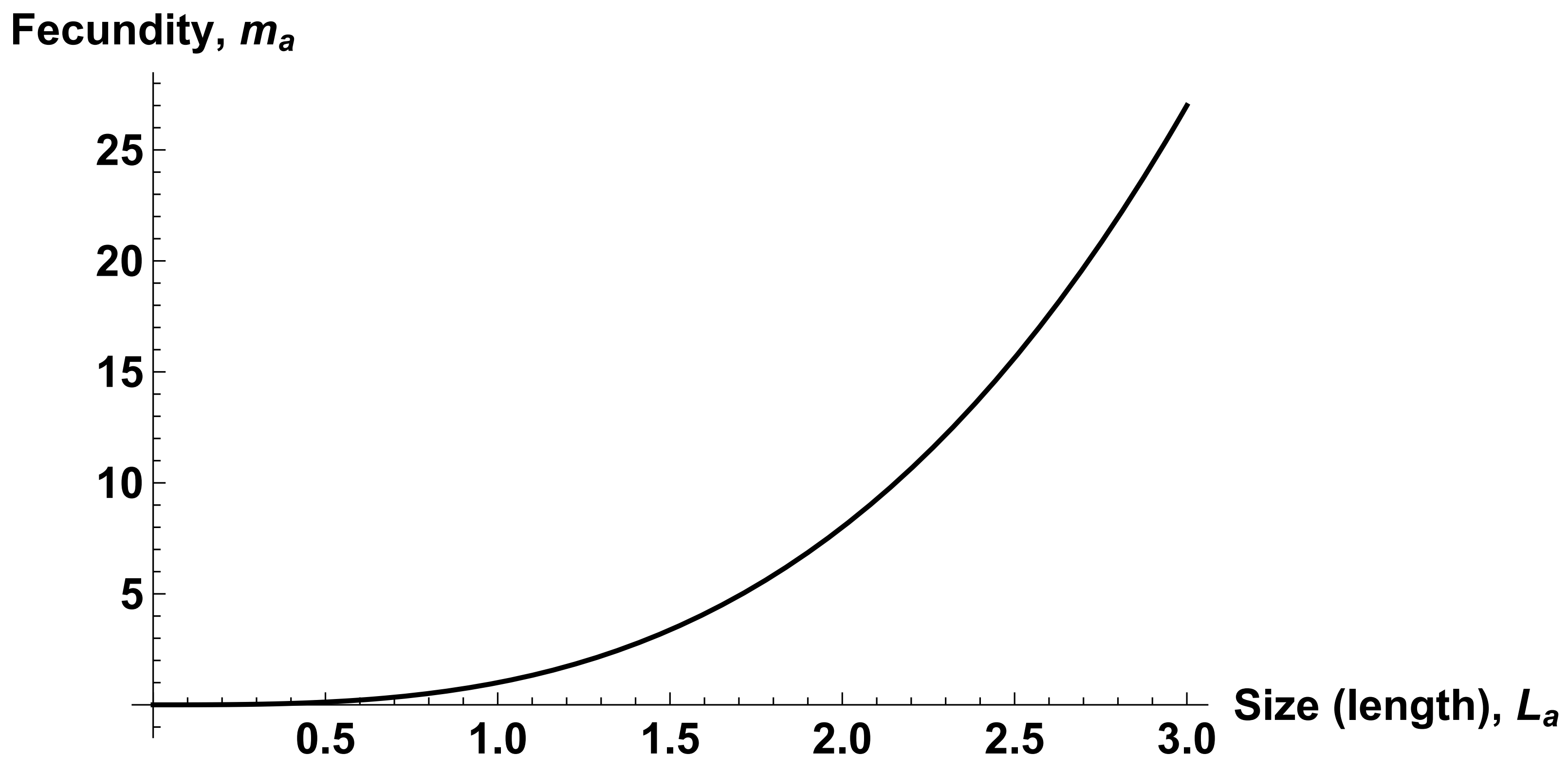


Effect of size at maturity
Roff's model (adapted)

- Age at maturity, *y*, evolving trait:

$$m_a(y,x) = \begin{cases} 0, & 1 \le a < y \\ cL_a(y)^3, & y \le a \end{cases}$$

where $L_a(y)$ is length at age *a* (so $L_a(y)^3$ is volume), which increases with *y*.



Von Bertalanffy growth equations

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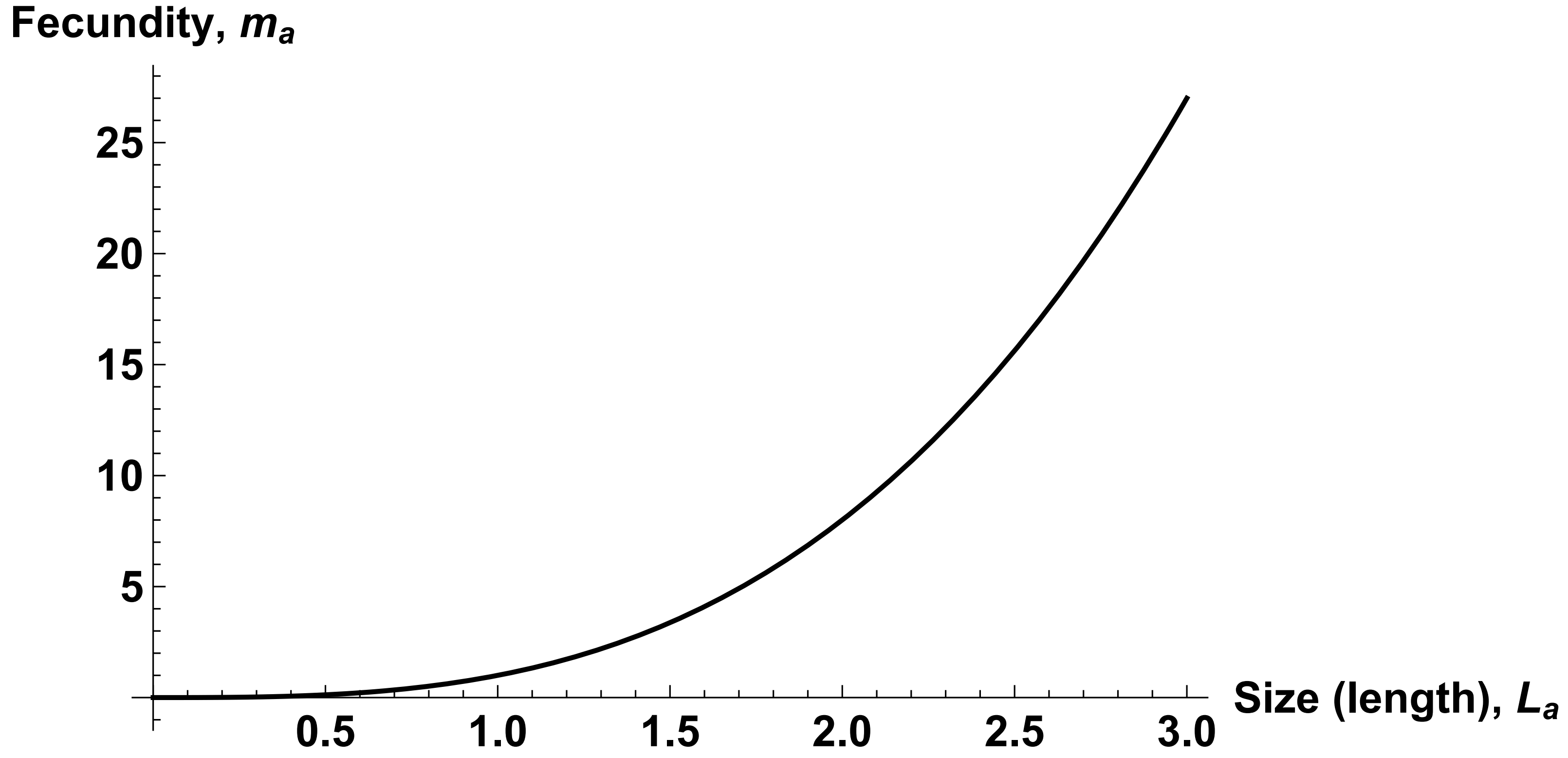

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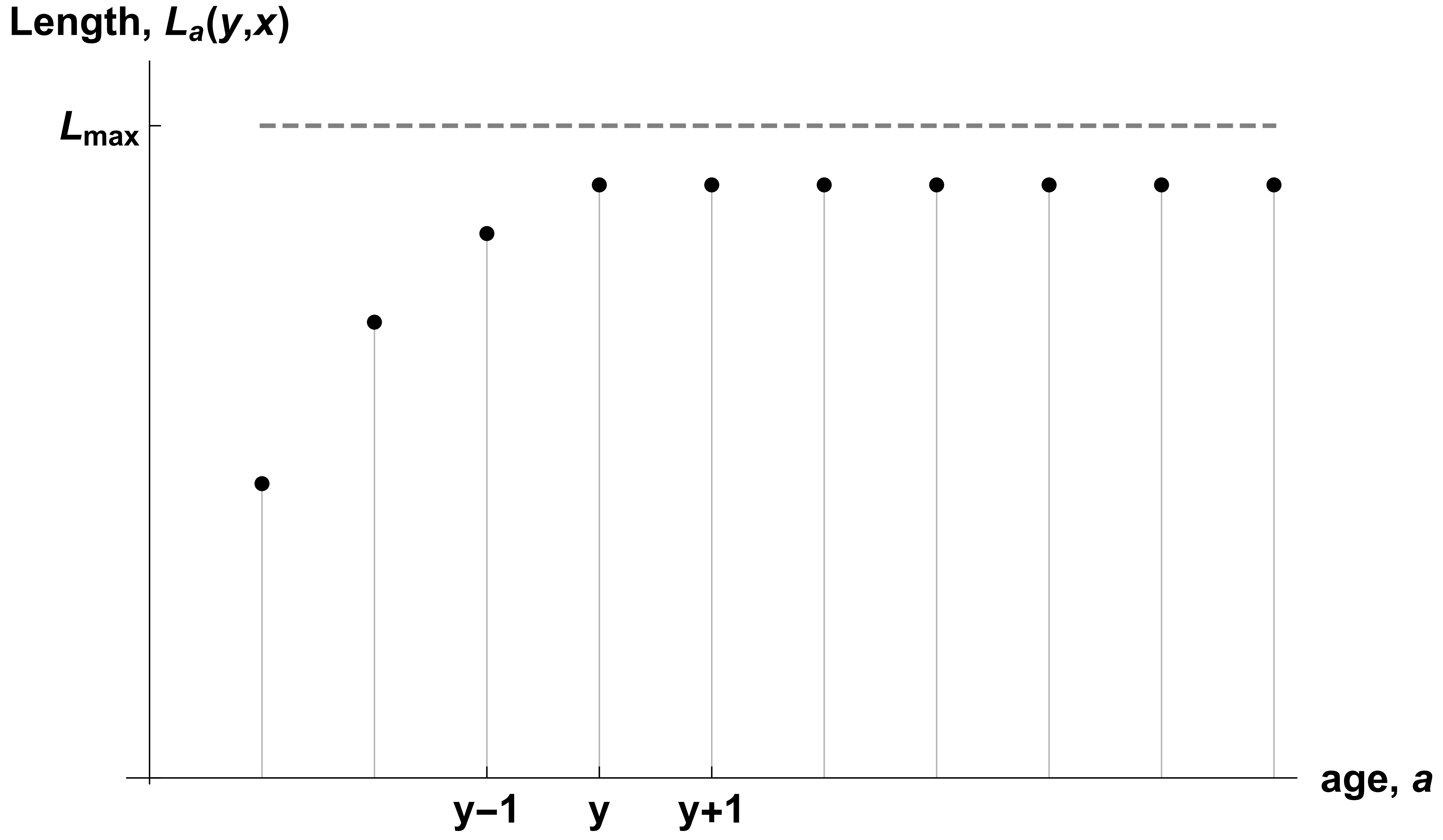

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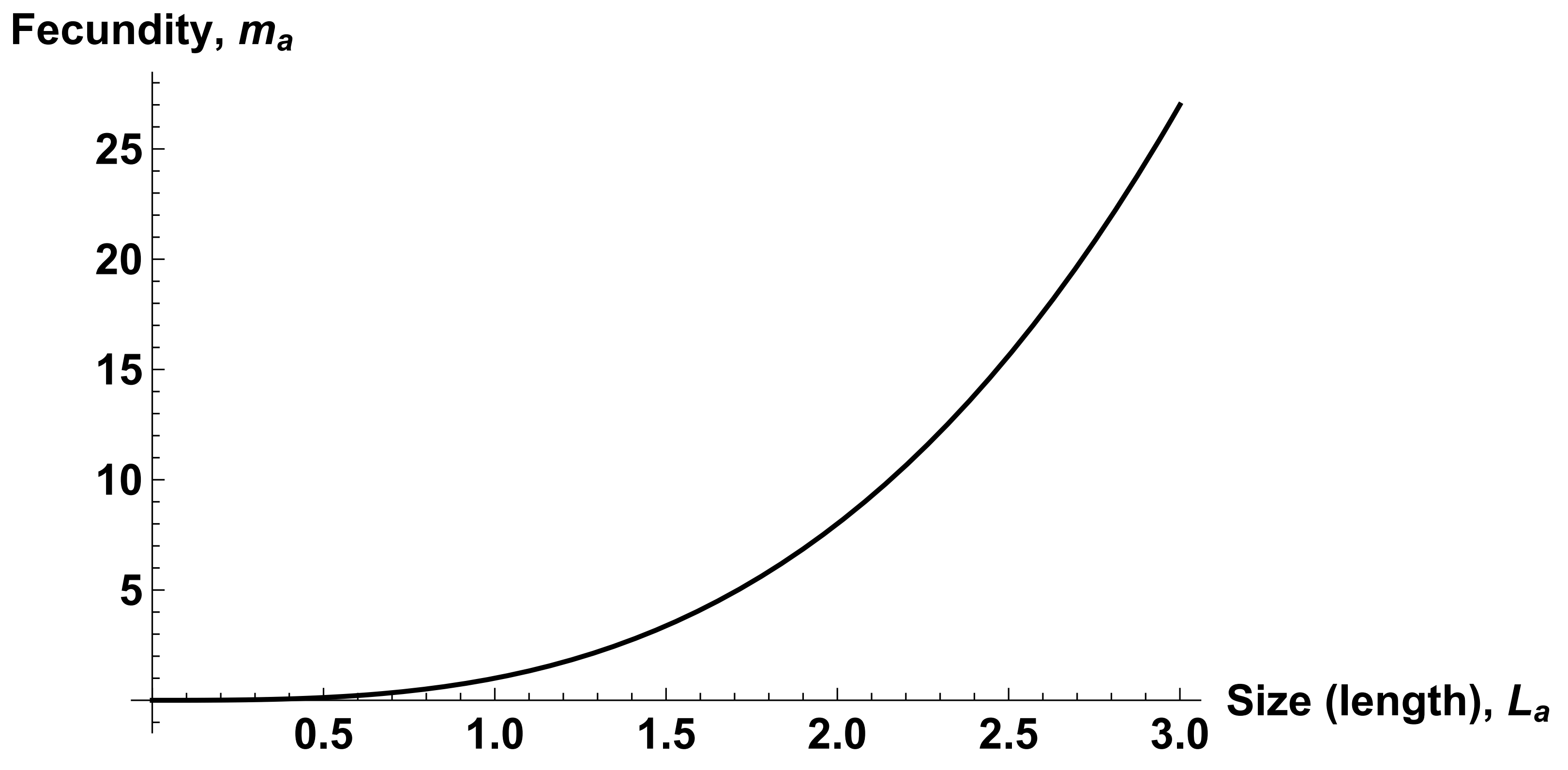

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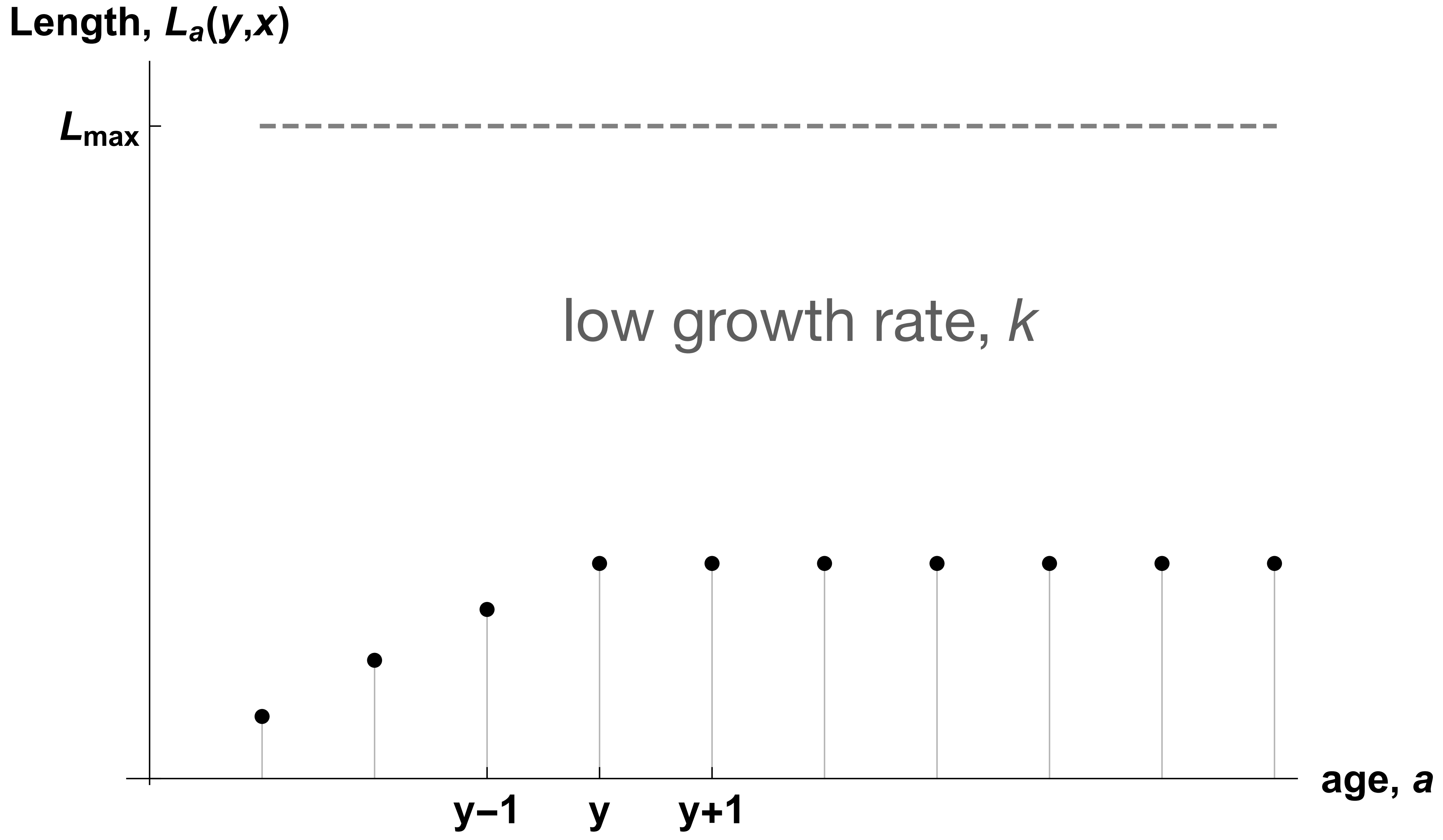

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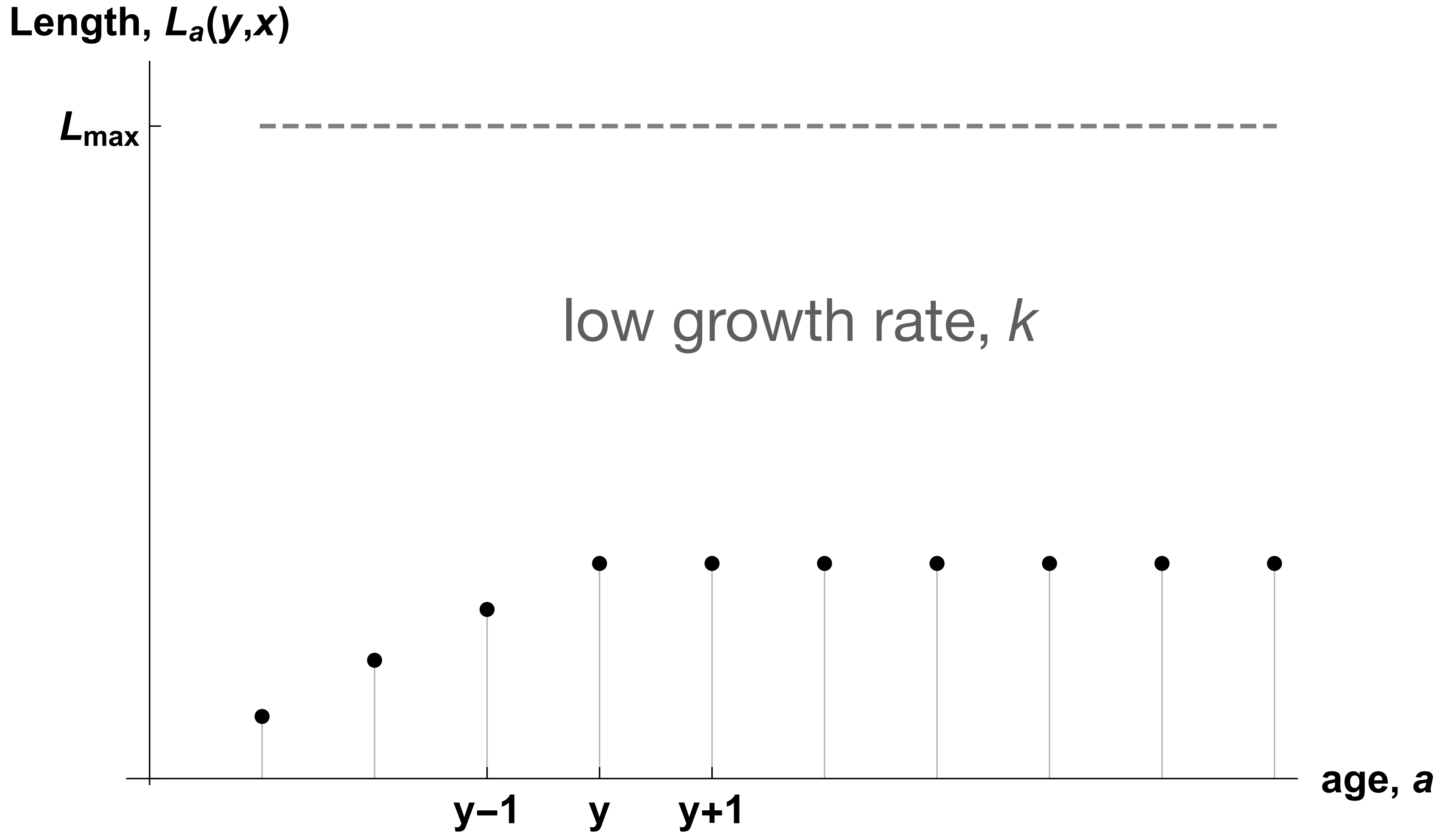

Mutant reproductive success

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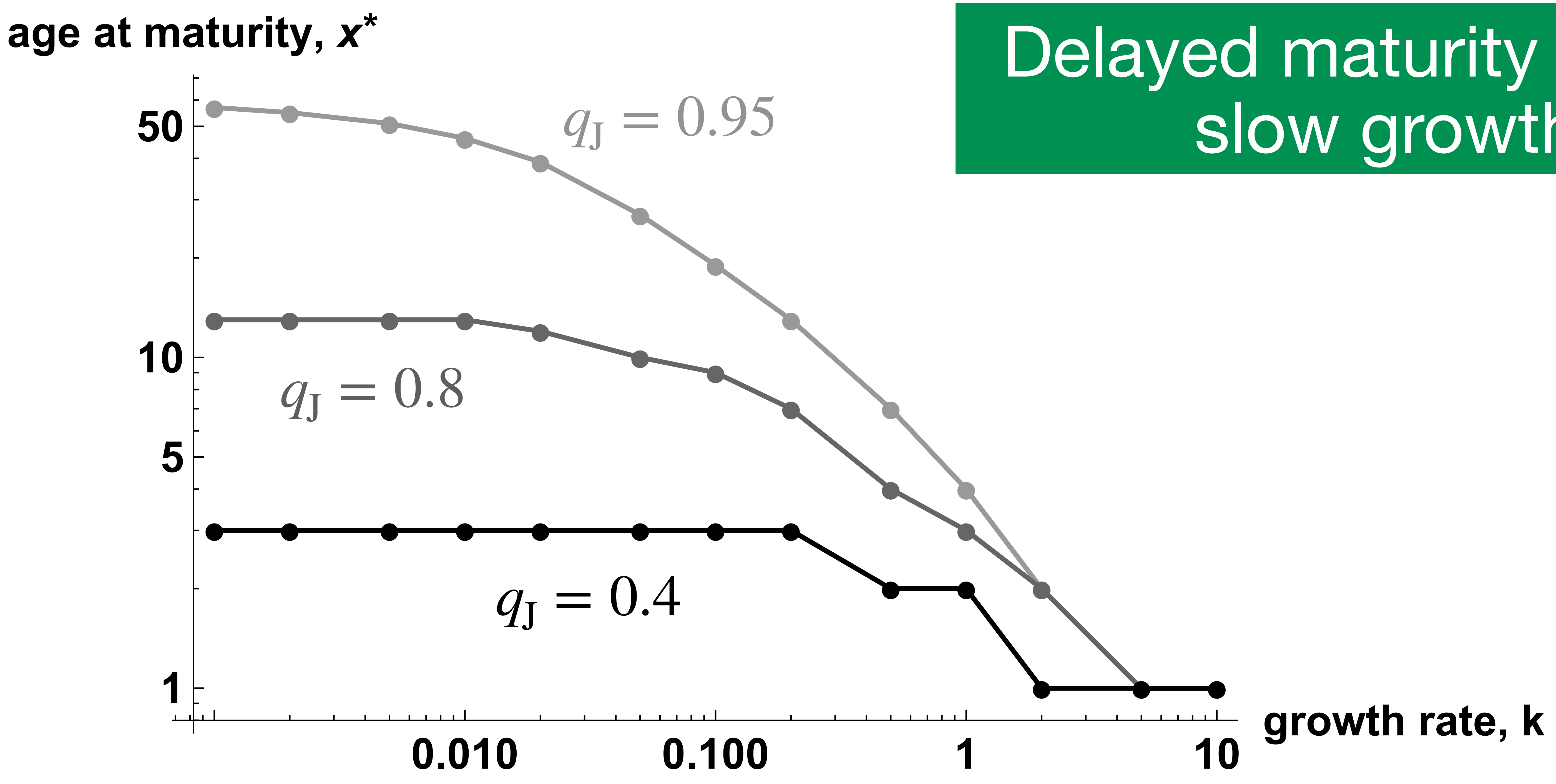
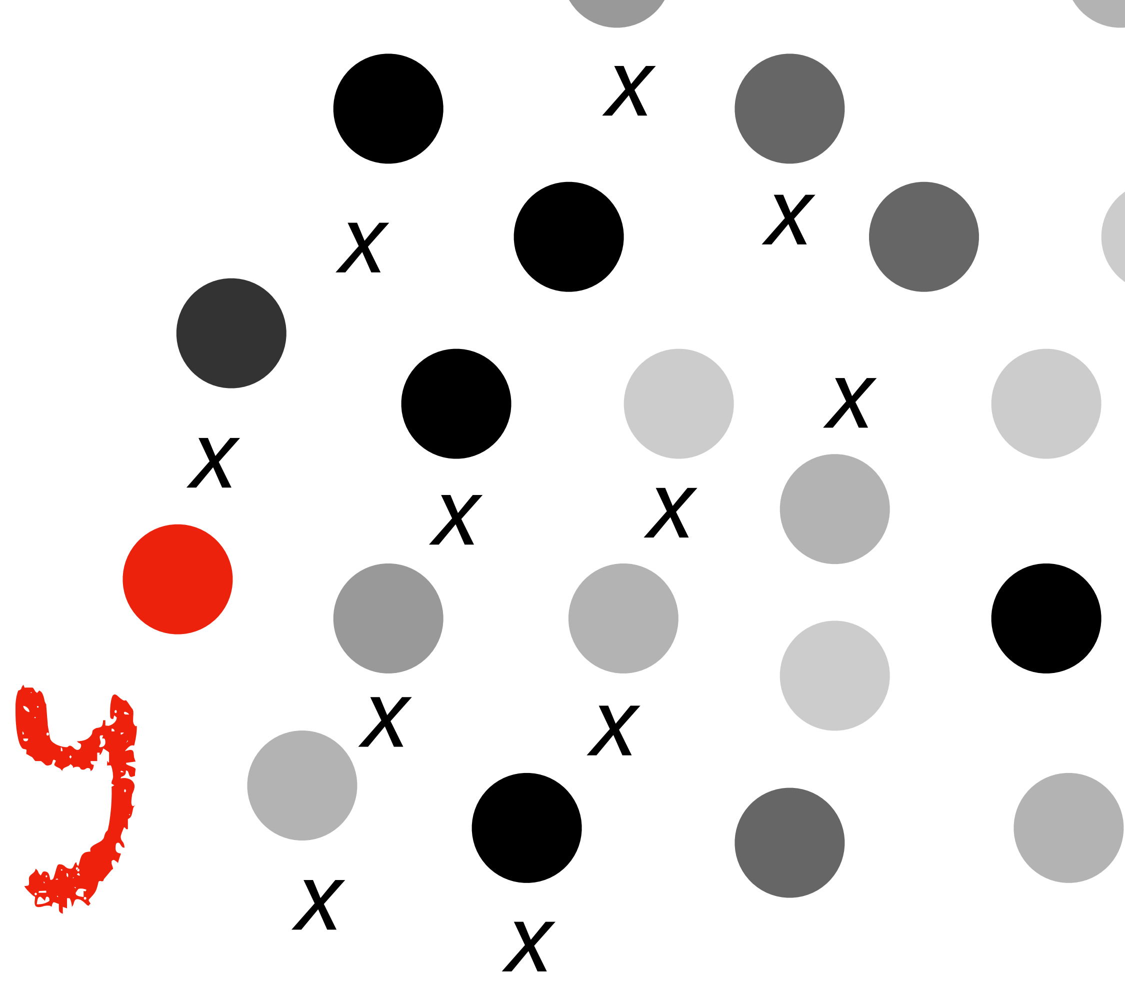
Optimal age at maturity



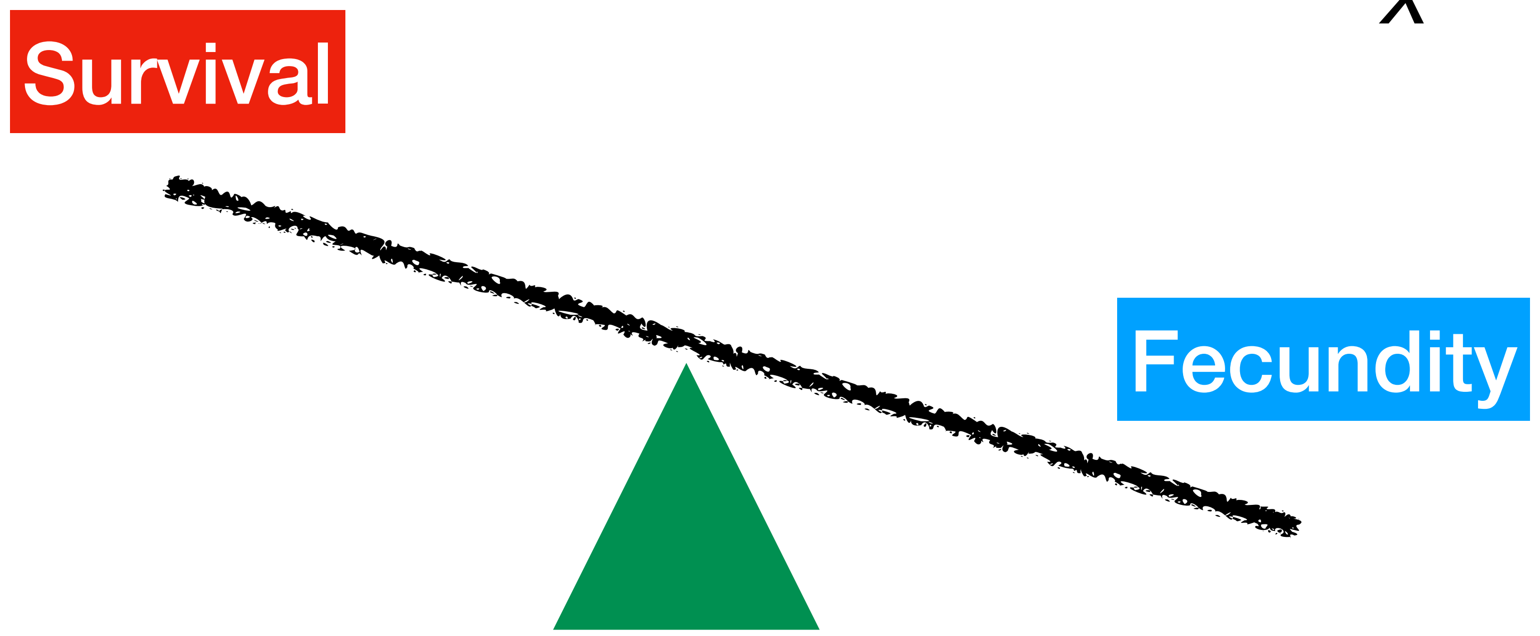
Delayed maturity favoured by slow growth rate.

Summary

Life history evolution

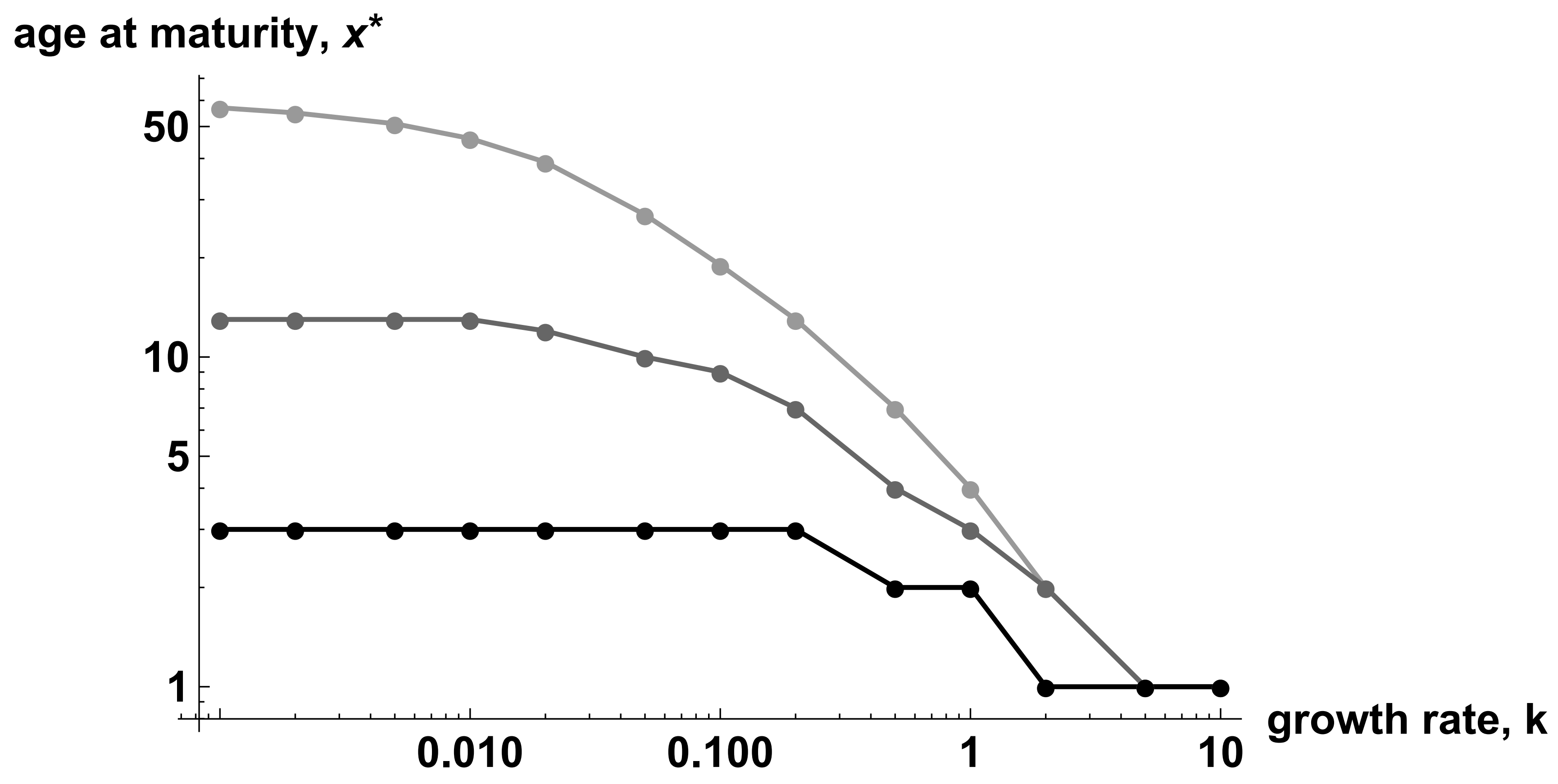


- Evolution of life history traits determined by **trade-offs** due to finite resources.



- Delayed maturity favoured by high survival till maturity and rapidly increasing fecundity.

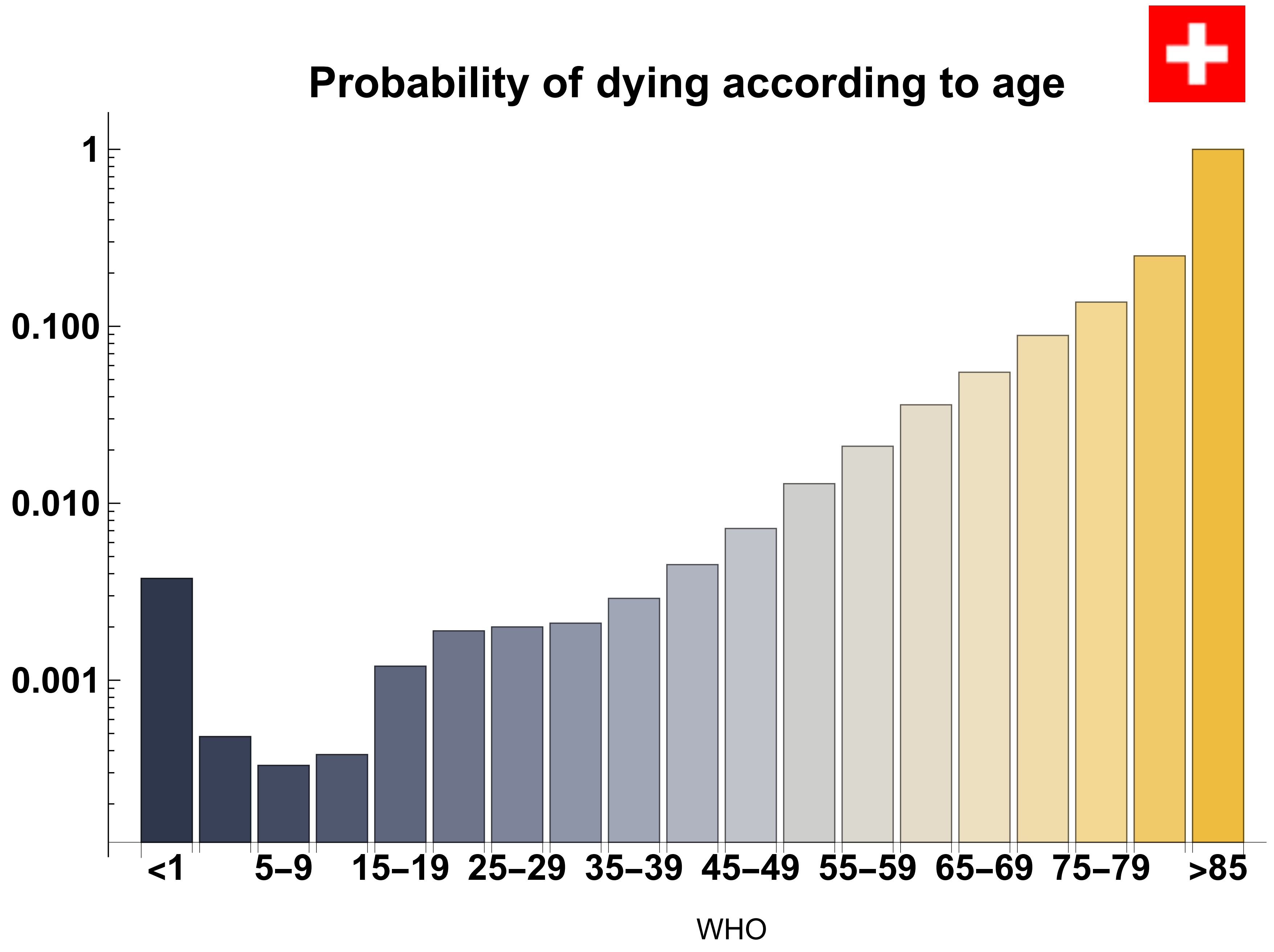
- Fecundity is often mediated by size (rather than age) so that delayed maturity favoured by slow growth.

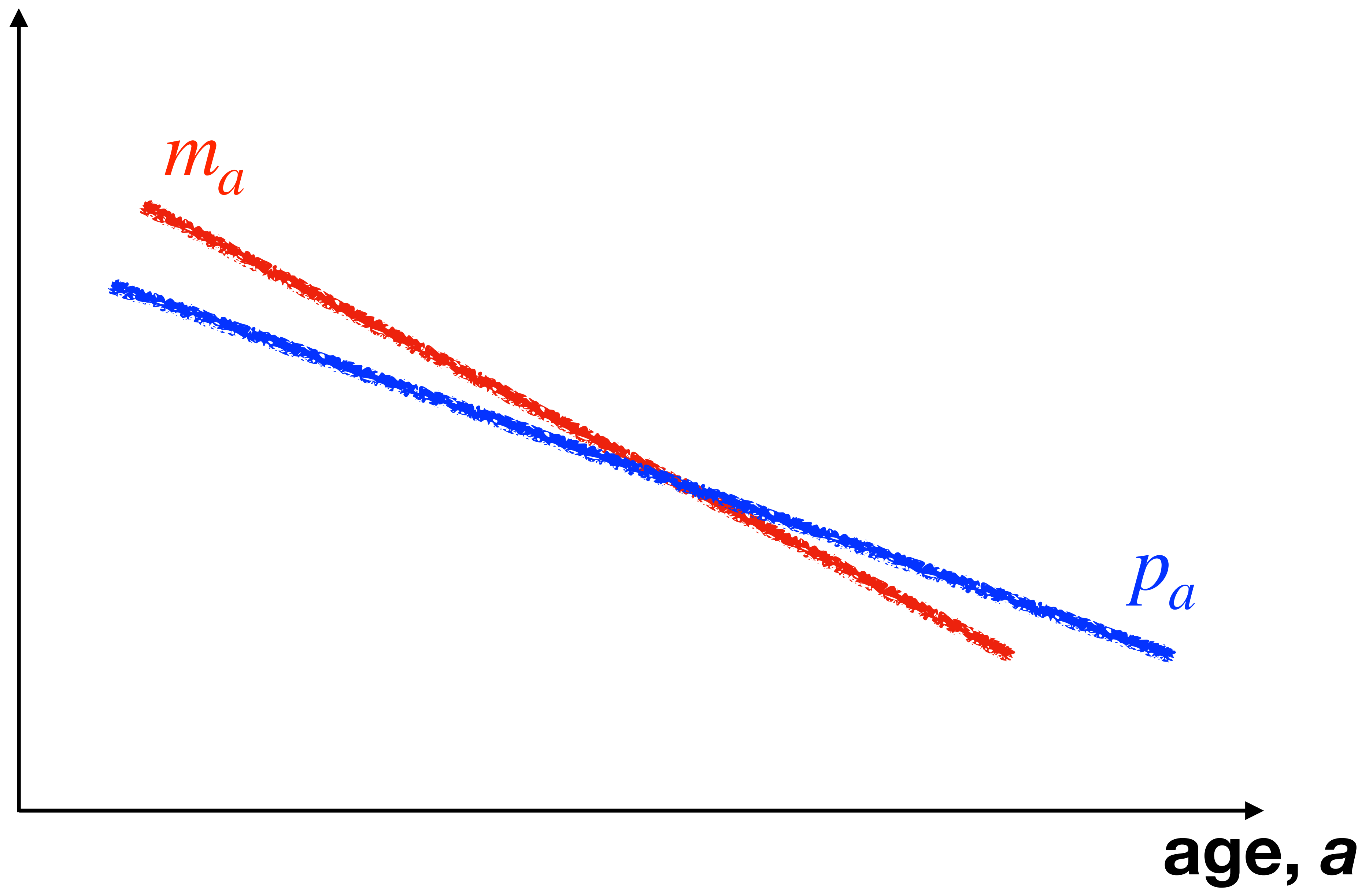


Evolution of ageing

Recap

- Gradual deterioration of function.
- Decrease in survival rate and/or fecundity with age.





Strength of selection on age specific traits

Hamilton 1966

$$R_0(y,x) = \sum_{a=1}^{\infty} l_a(y,x) m_a(y,x)$$

$$l_a(y,x) = p_0(y,x) p_1(y,x) \ldots p_{a-1}(y,x)$$

$$s(x) = \left. \frac{\partial R_0(y,x)}{\partial y} \right|_{y=x}$$

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$$l_a(y,x) = p_0(y,x) p_1(y,x) \ldots p_{a-1}(y,x)$$

$$s(x) = \left.\frac{\partial R_0(y,x)}{\partial y}\right|_{y=x} = \sum_{a=0}^{\infty} l_a(x) \left[\left.\frac{\partial m_a(y,x)}{\partial y}\right|_{y=x} + \left.\frac{\partial p_a(y,x)}{\partial y}\right|_{y=x} v_{a+1}(x) \right]$$

reproductive value of age a+1, i.e. expected number of offspring given survival till age a+1 $= v_{a+1}(x) = \sum_{b=a+1}^{\infty} \frac{l_b(x)}{l_{a+1}(x)} m_b(x)$

Strength of selection decreases with age

Hamilton 1966

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selection on survival proportional to reproductive value

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Gray squirrel example (with fecundity scaled so that $R_0 = 1$)

Age *a* (years)	p_a	m_a	f_a
0	0.25		
1	0.46	1.15	0.32
2	0.77	2.05	0.57
3	0.65	2.05	0.57
4	0.67	2.05	0.57
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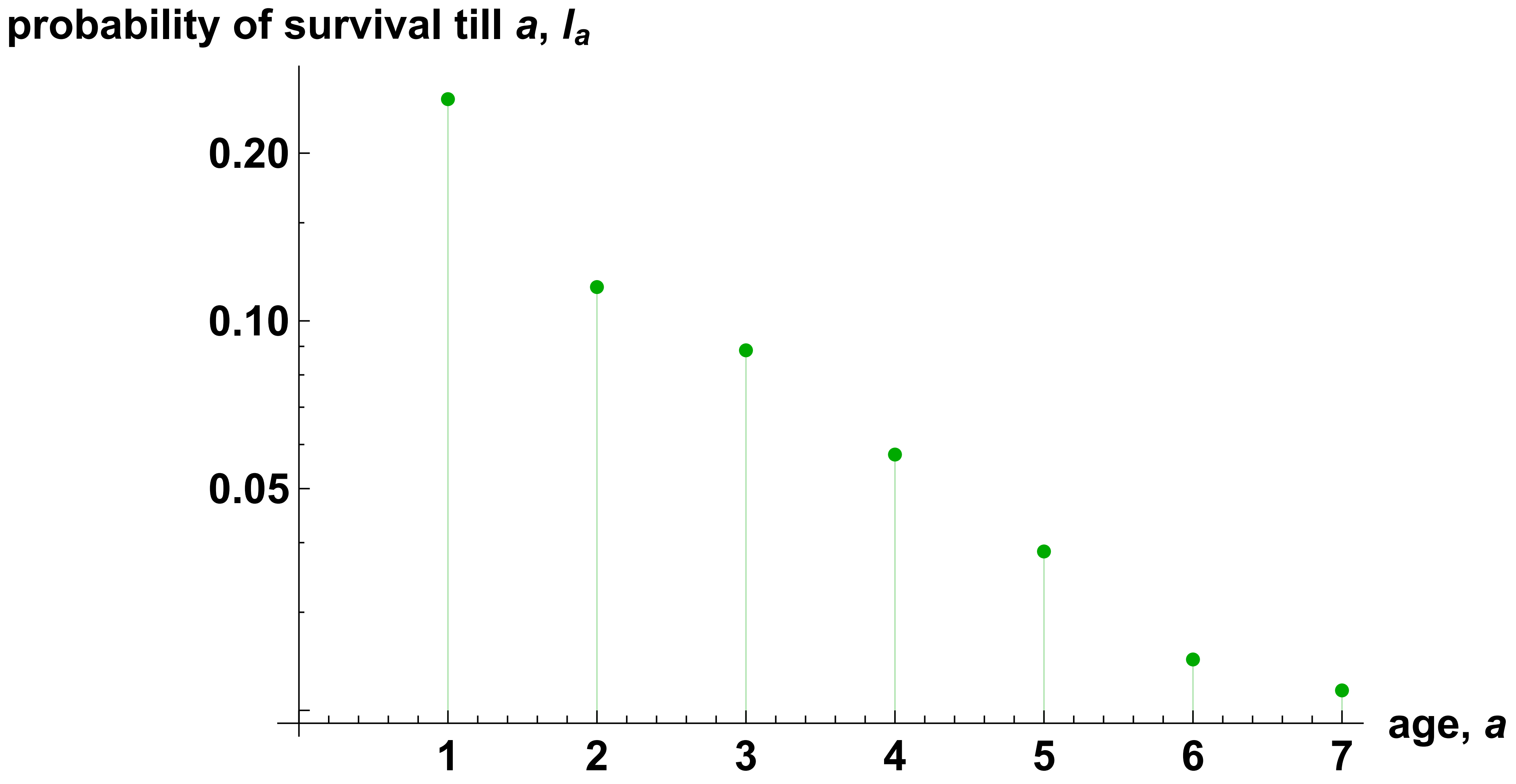

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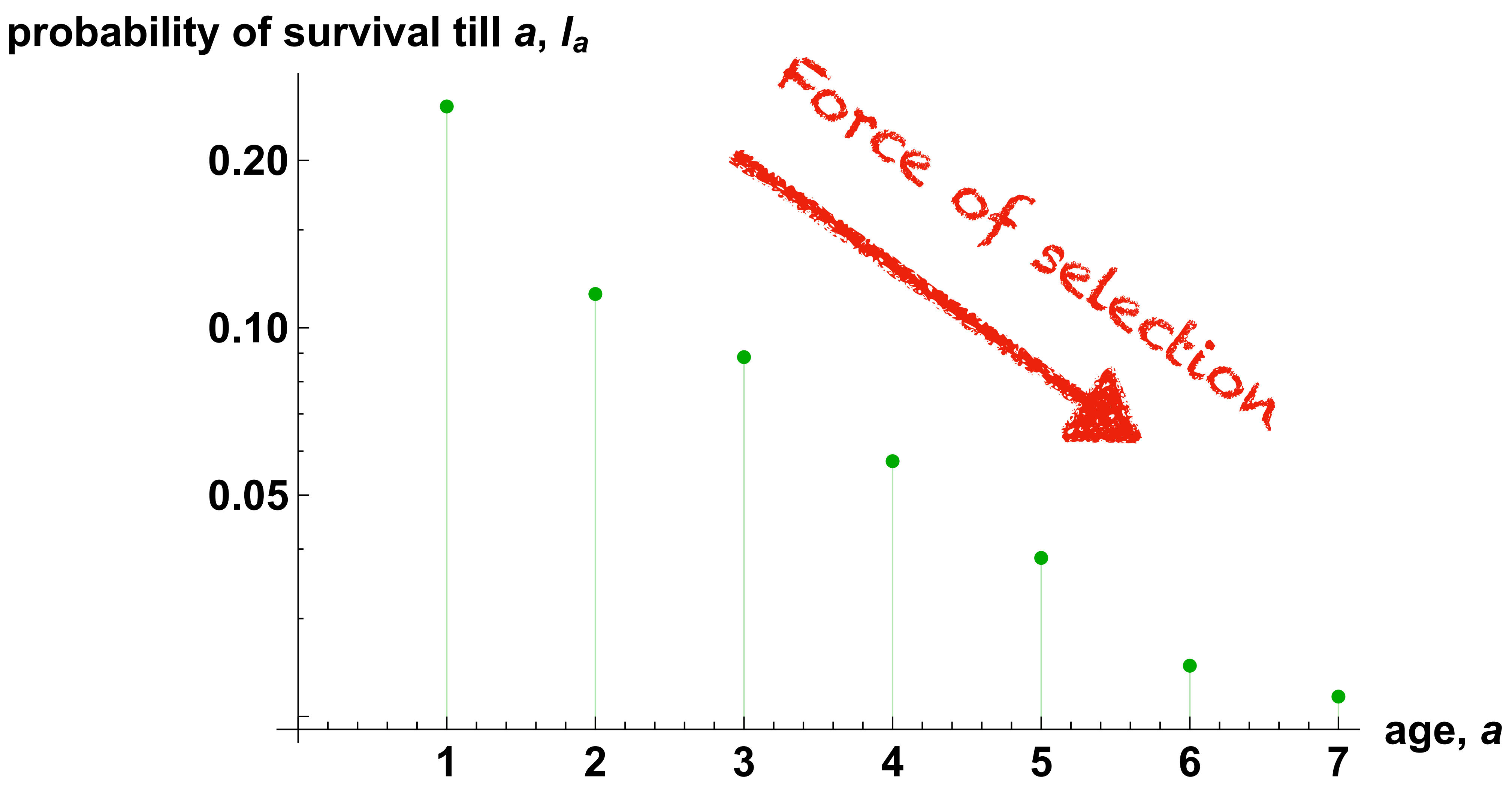

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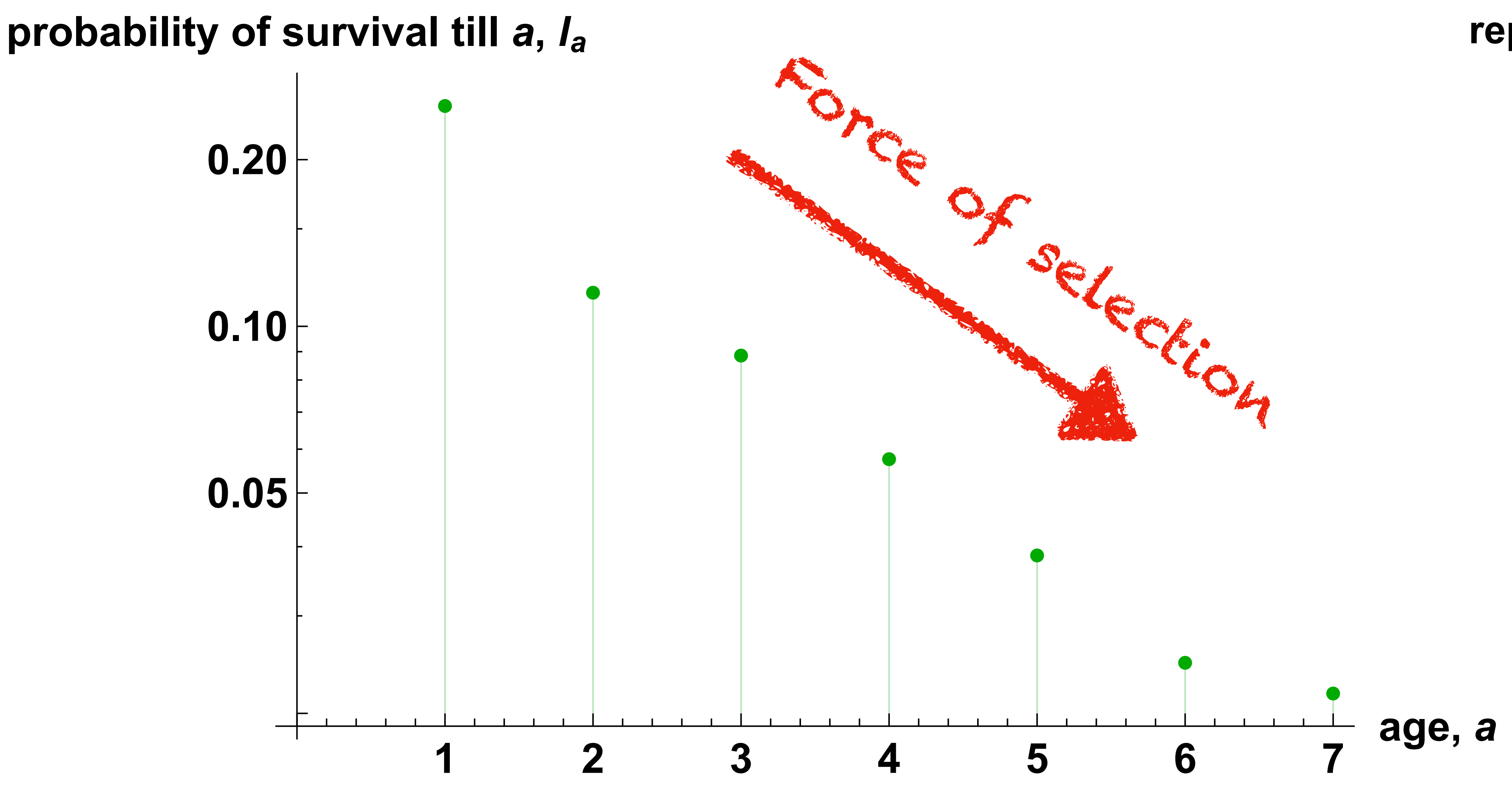
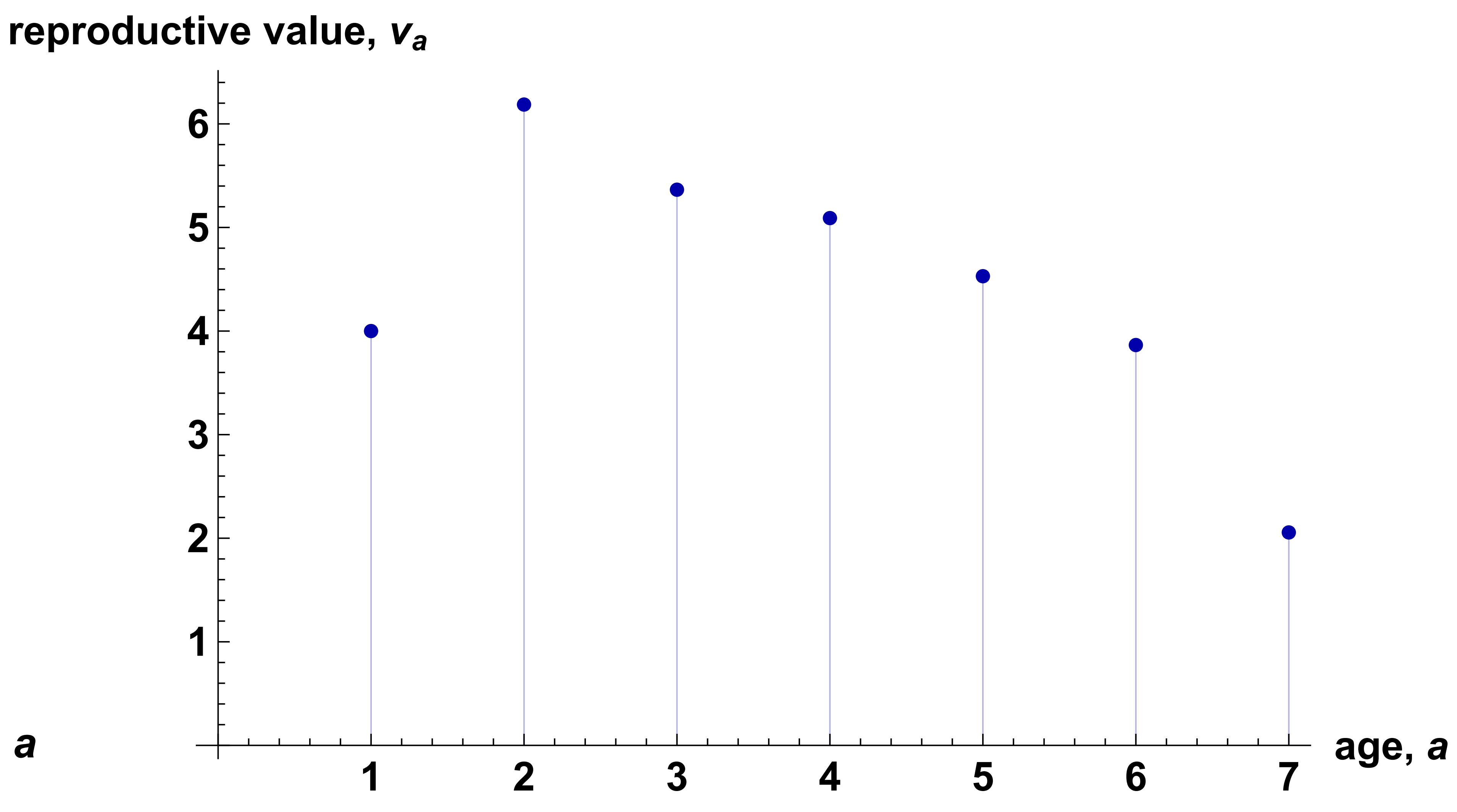


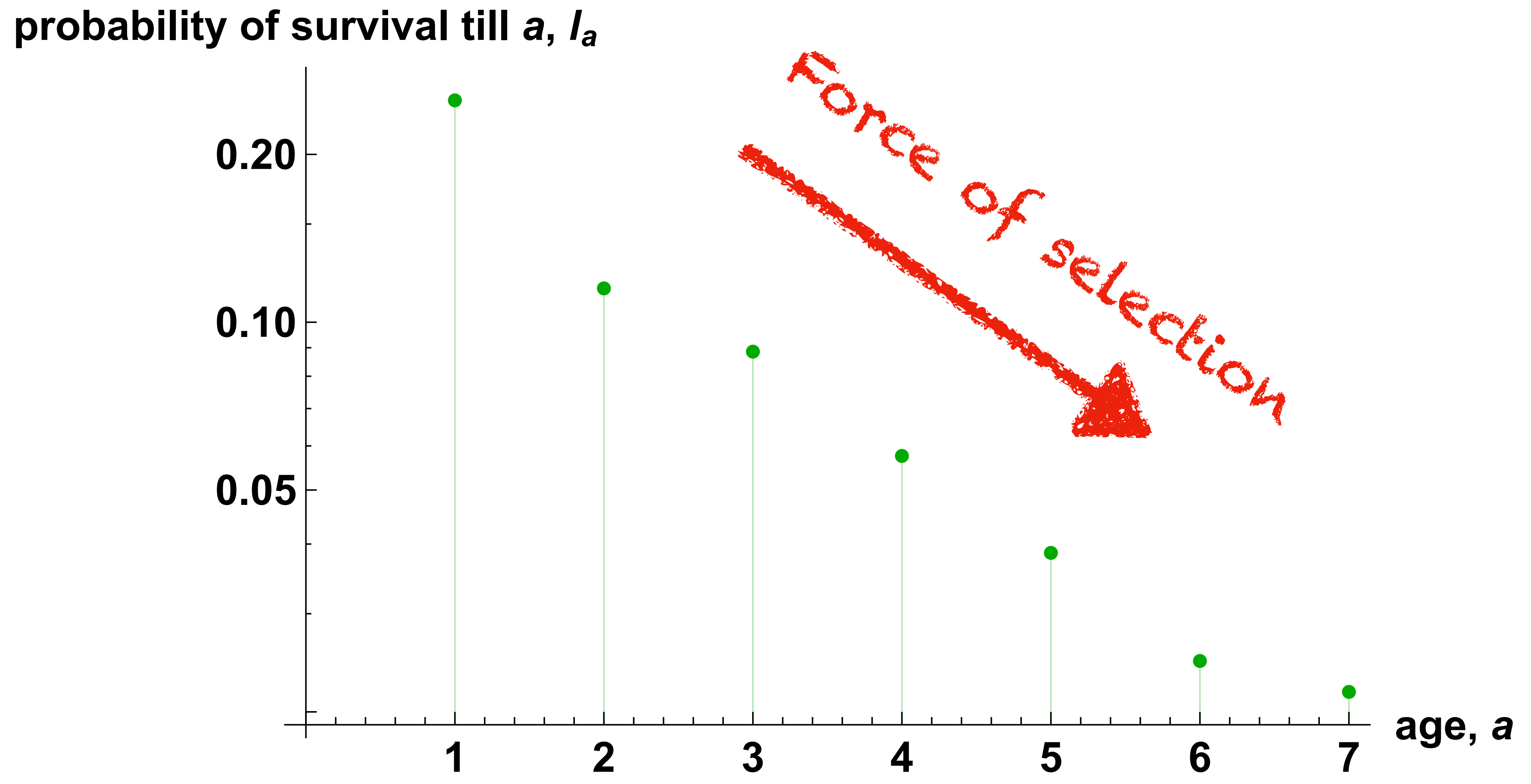


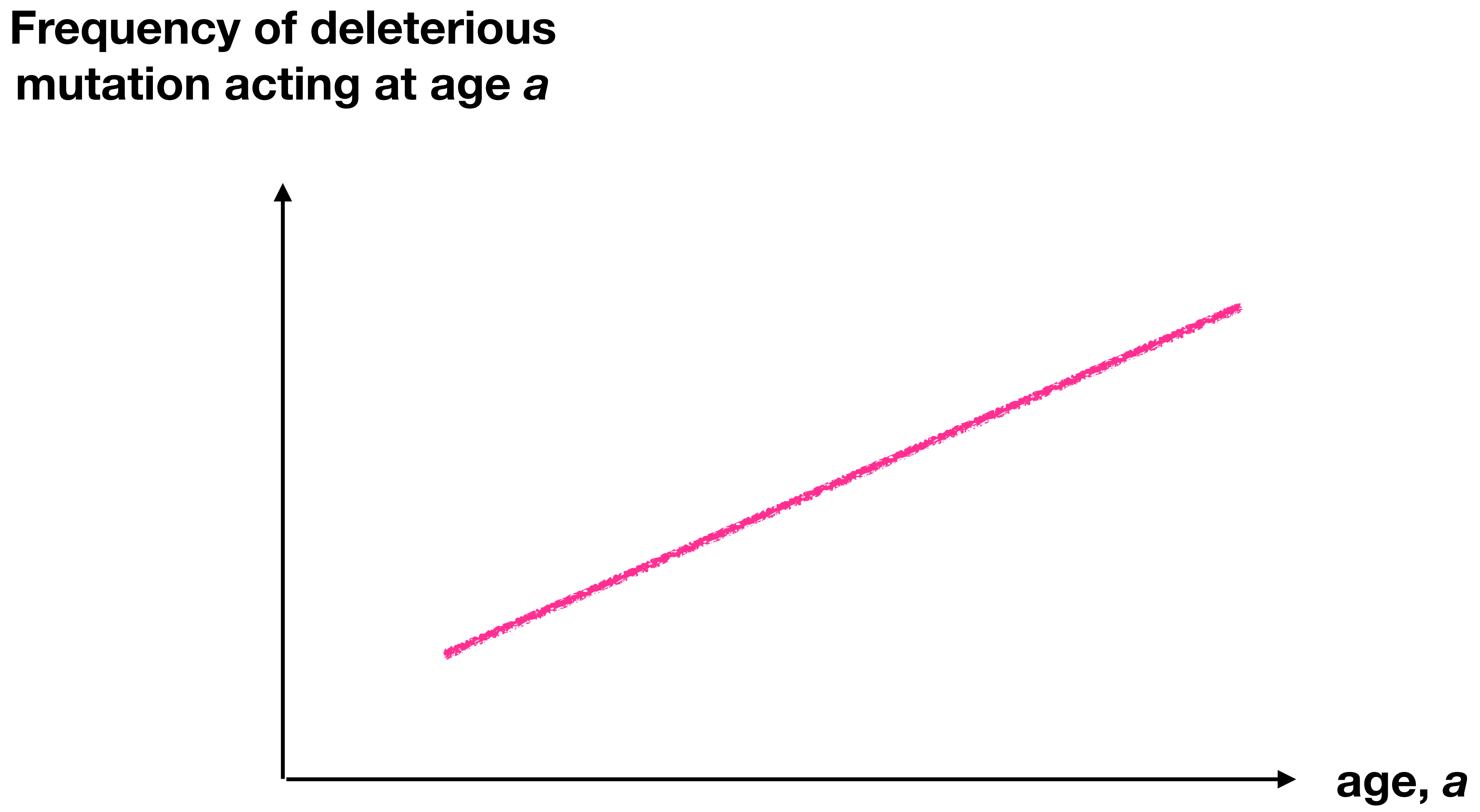
selection on fecundity decreases with age

selection on survival biased towards ages with greatest perspective of reproduction

Mutation accumulation
Medawar 1952

- Deleterious, late-acting mutations accumulate with little resistance as selection weakens with age of action.
- Causes a reduction in vital rates with age.





Antagonistic pleiotropy
Williams 1957

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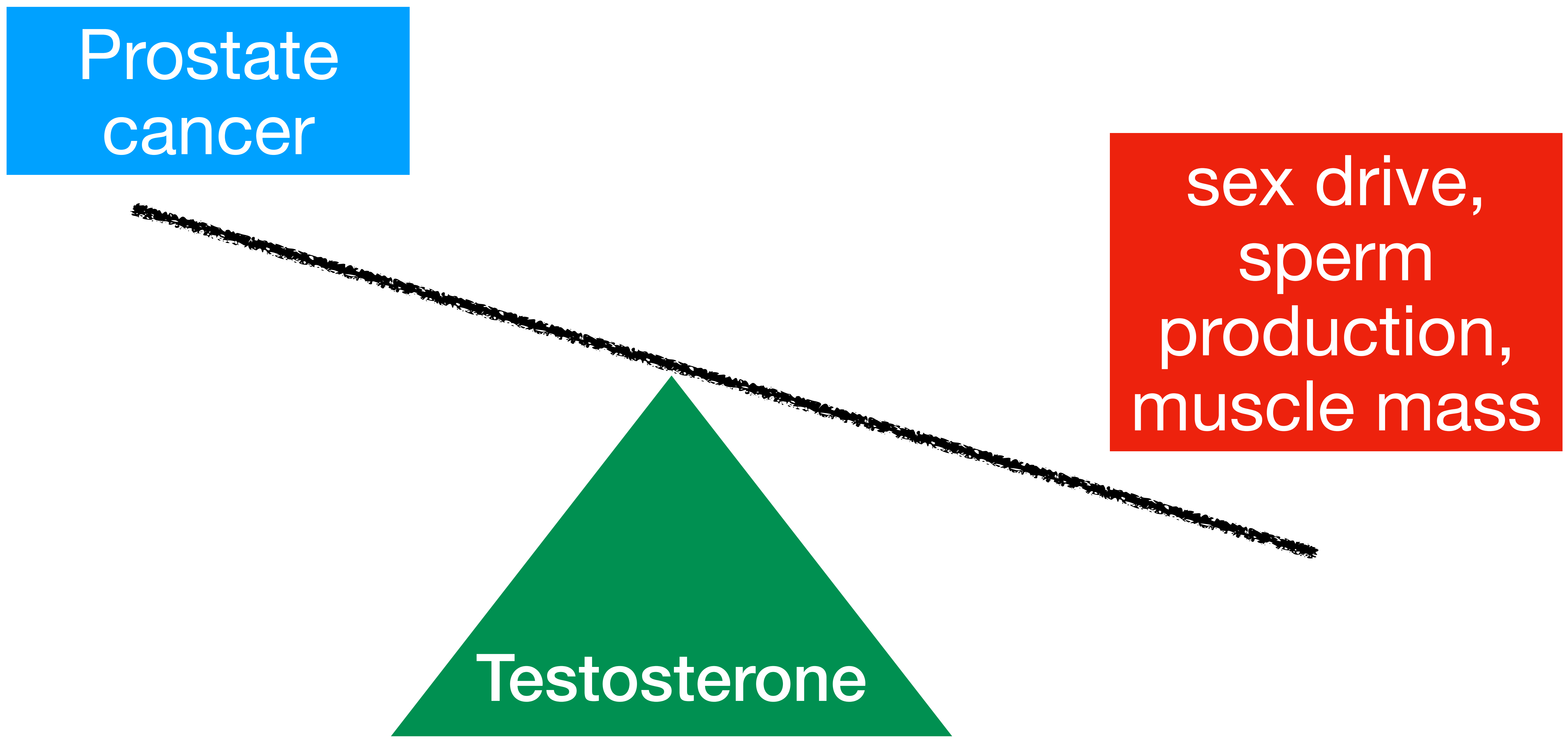

Disposable soma theory
Kirkwood 1977

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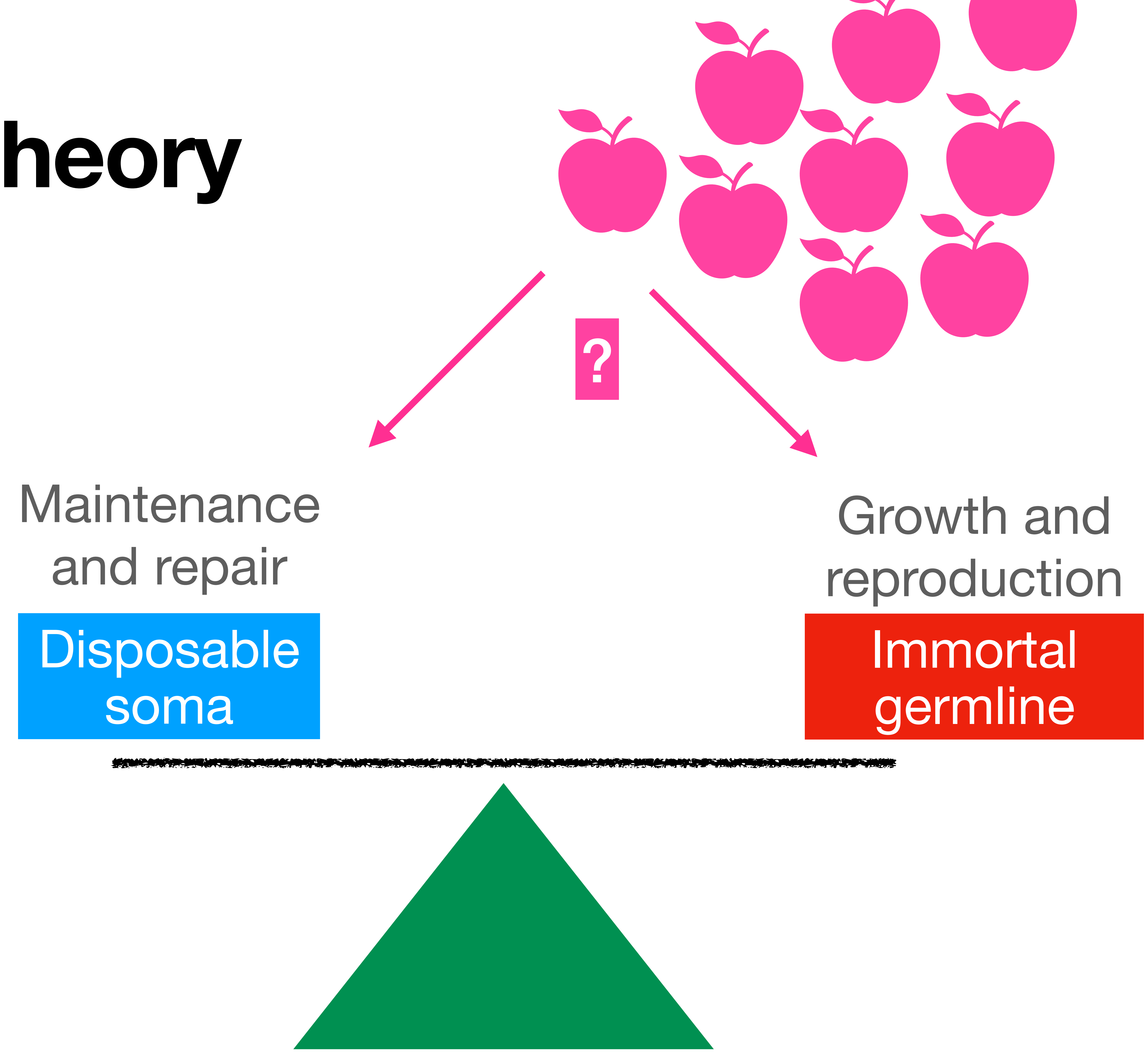

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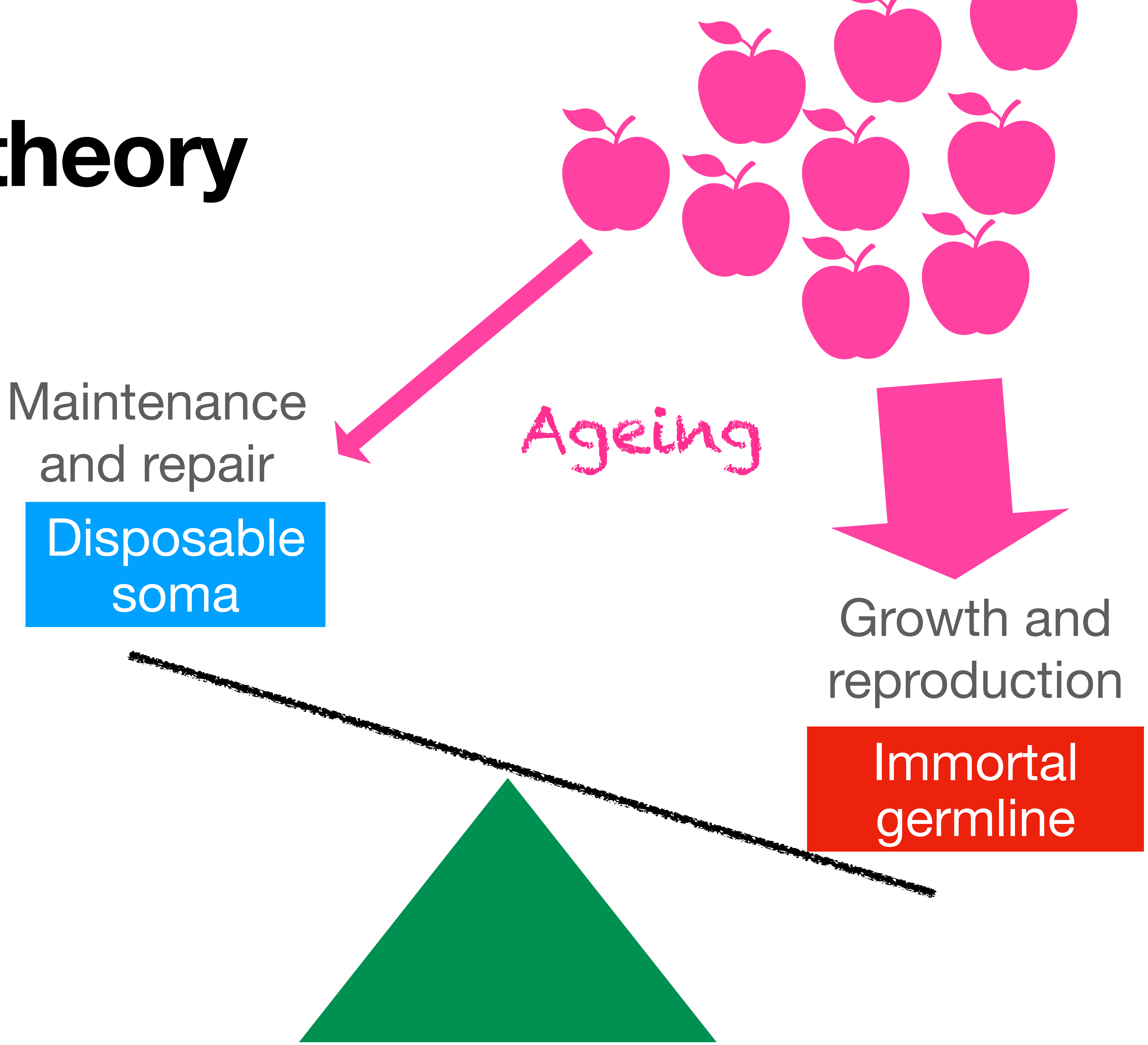

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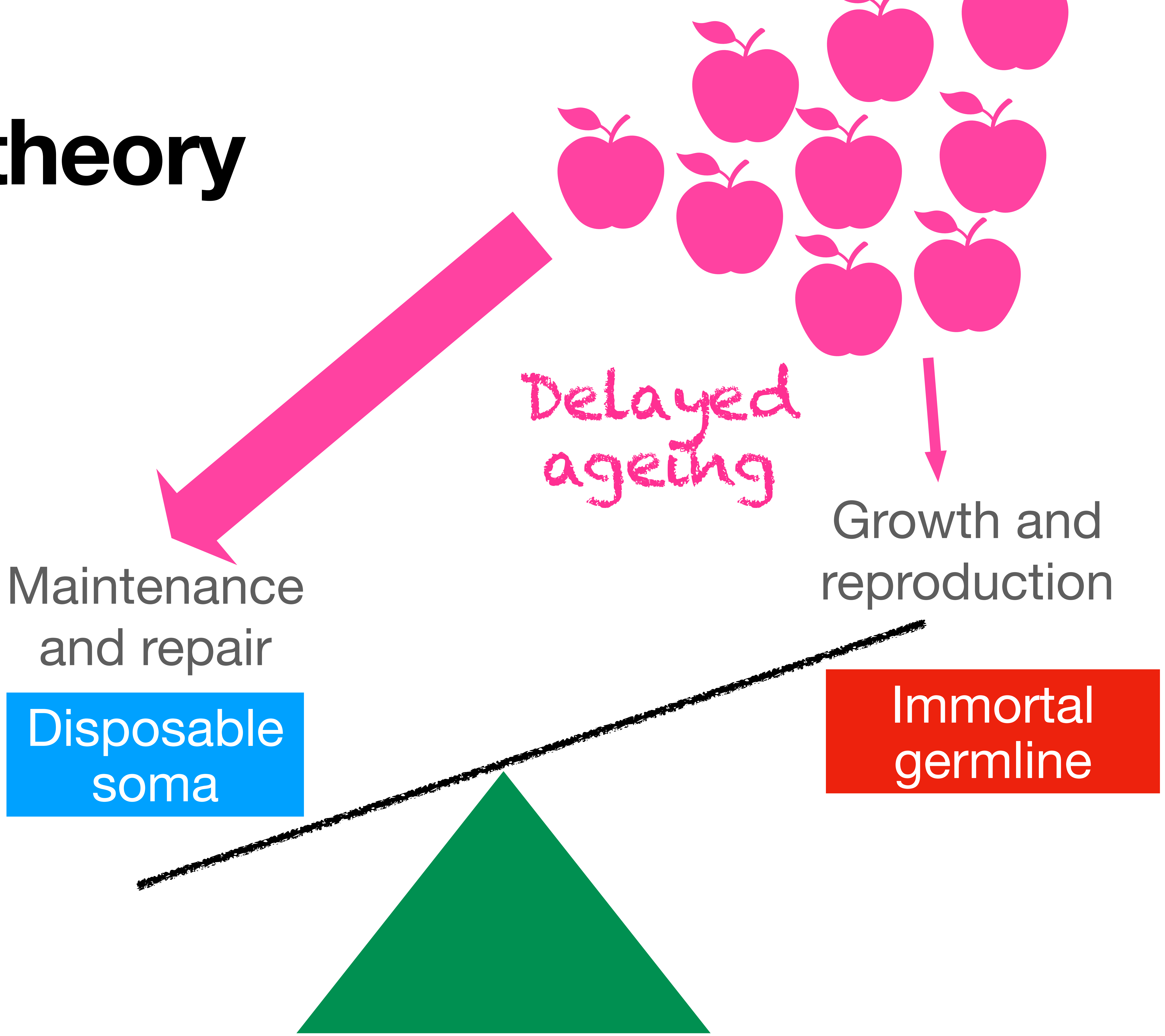

Summary

selection on senescence

- Strength of selection on traits with age-specific effects declines with age (proportional to probability of surviving till relevant age)
- Selection on traits influencing age-specific survival also proportional to reproductive value
- Two non-exclusive theories for ageing:
  - Mutation accumulation (selection too weak to purge detrimental mutations with late effects)
  - Antagonistic pleiotropy (favours early effects at the expense of later effects)