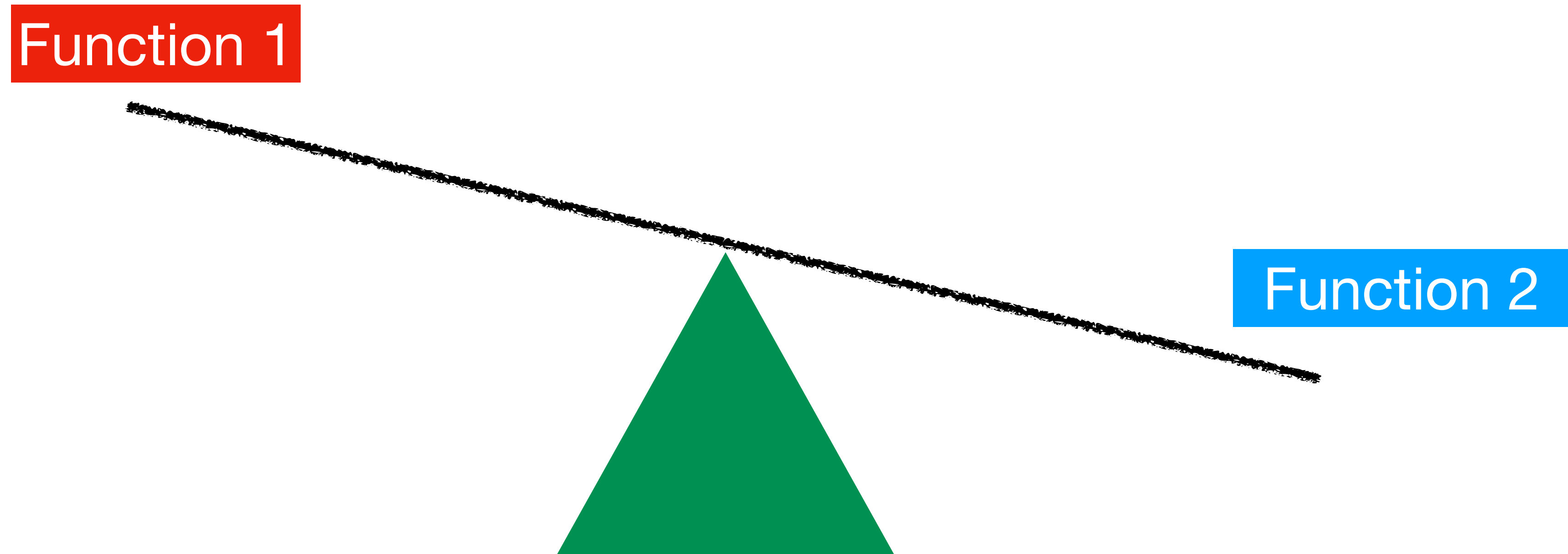


# Life-history evolution



# Trade offs

due to finite resources



# Example

**Fecundity *vs.* offspring survival**

# Example

## Fecundity vs. offspring survival

- 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.



# Example

## Fecundity vs. offspring survival

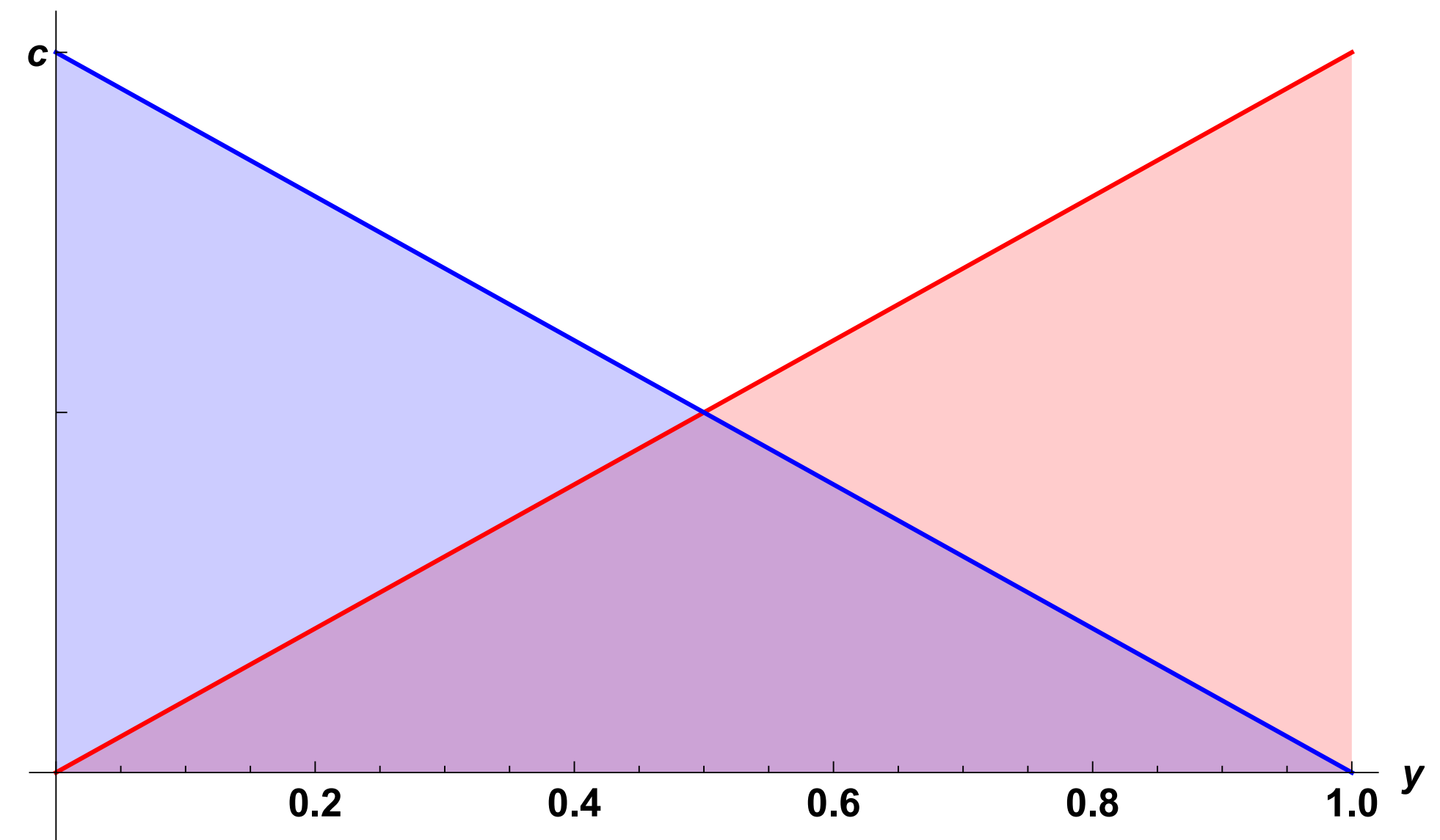
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- Fecundity at age 1 of a mutant investing  $y$ :

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

- Offspring survival from age 0 to 1:

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

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



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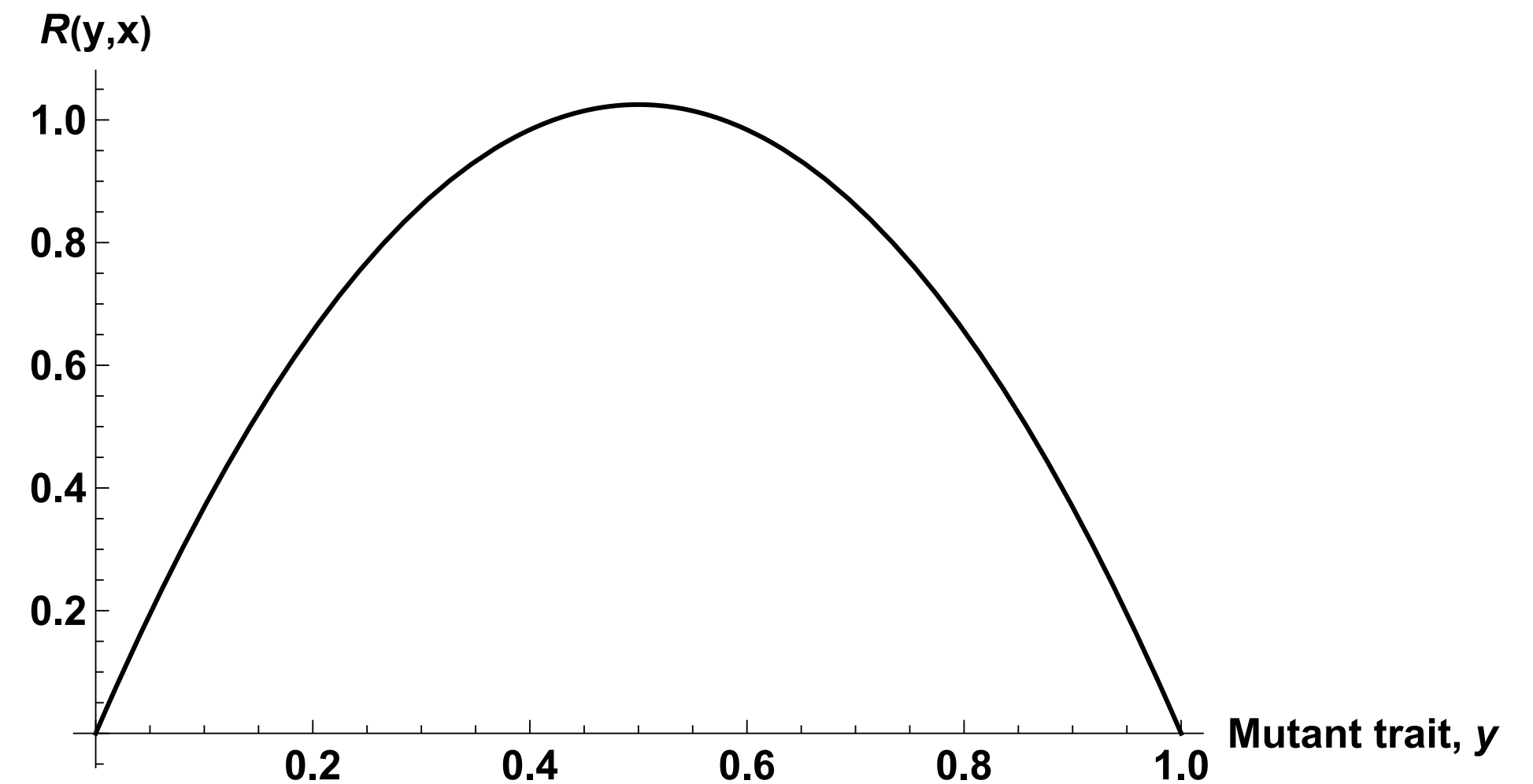
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- Lifetime reproductive success:

$$R_0(y, x) = \sum_{a=1}^1 l_a(y, x)m_a(y, x) = (1 - y)K(x) \times cy$$



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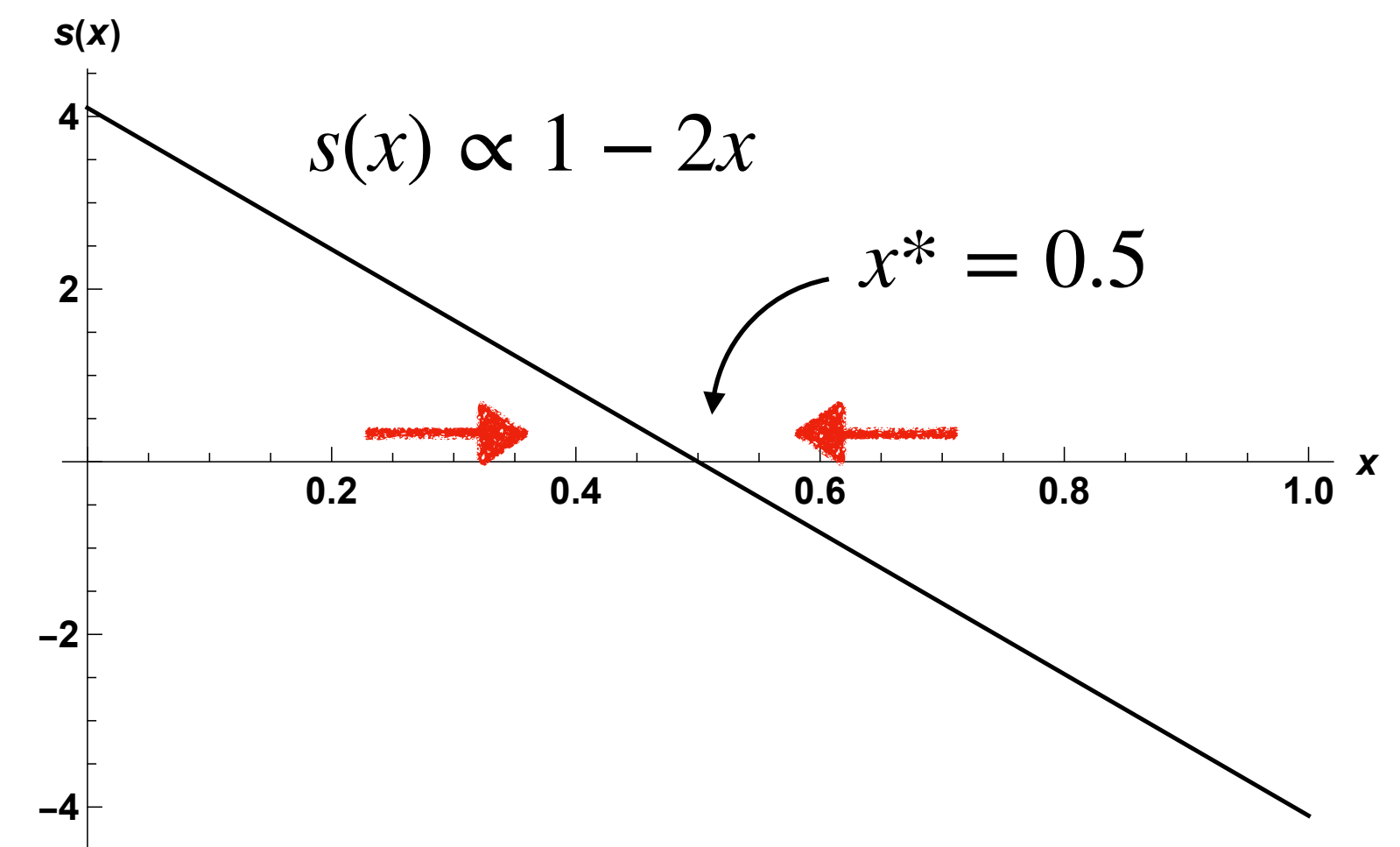
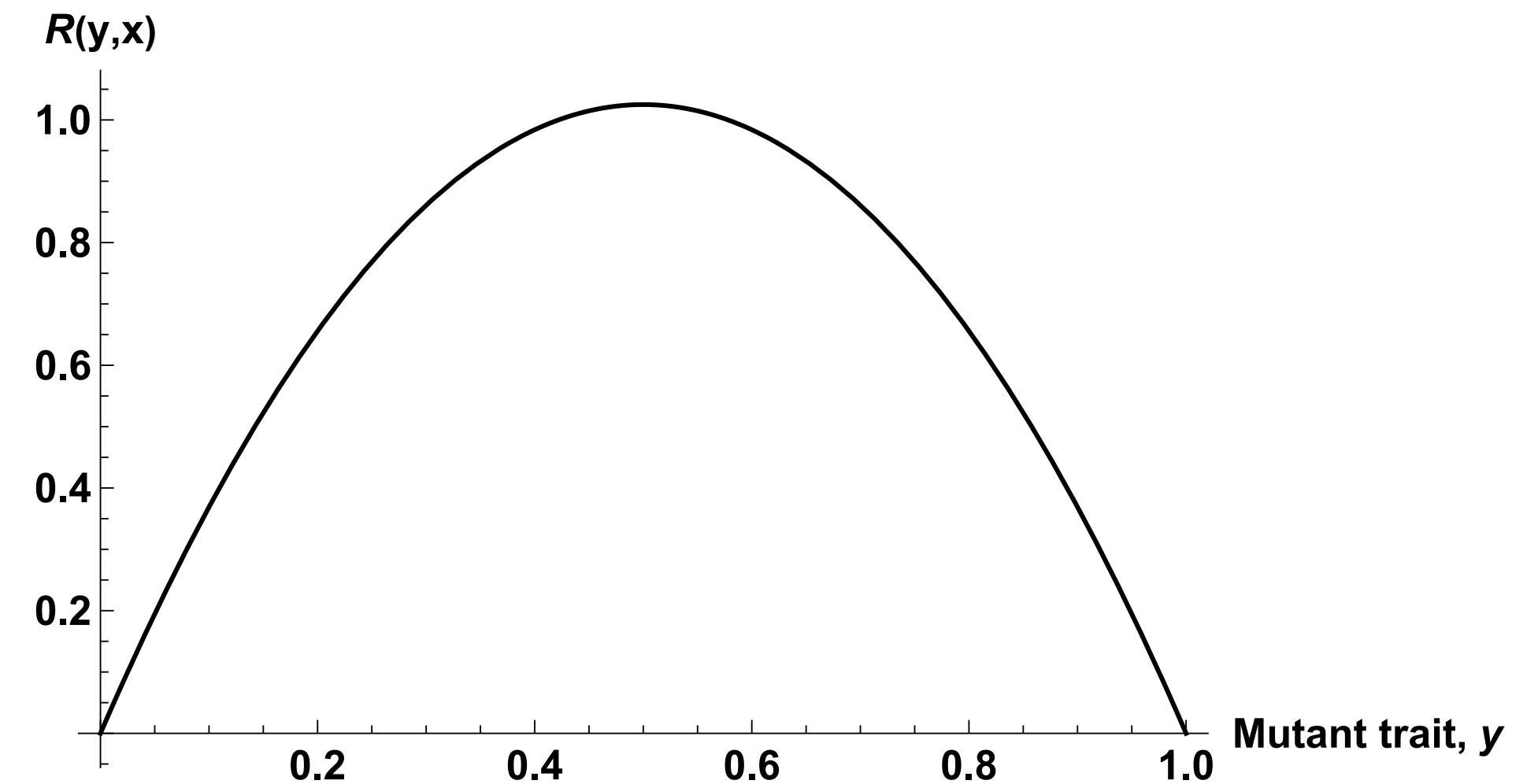
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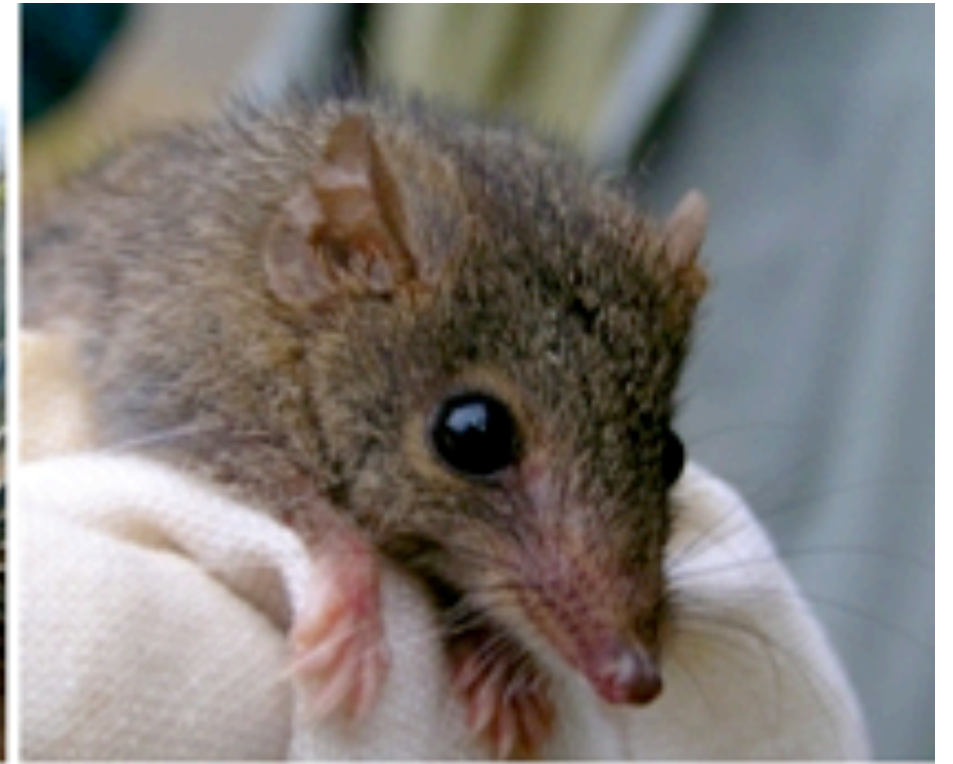




# Iteroparity vs. semelparity

## Exercise sheet - Trade off between adult survival and fecundity

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



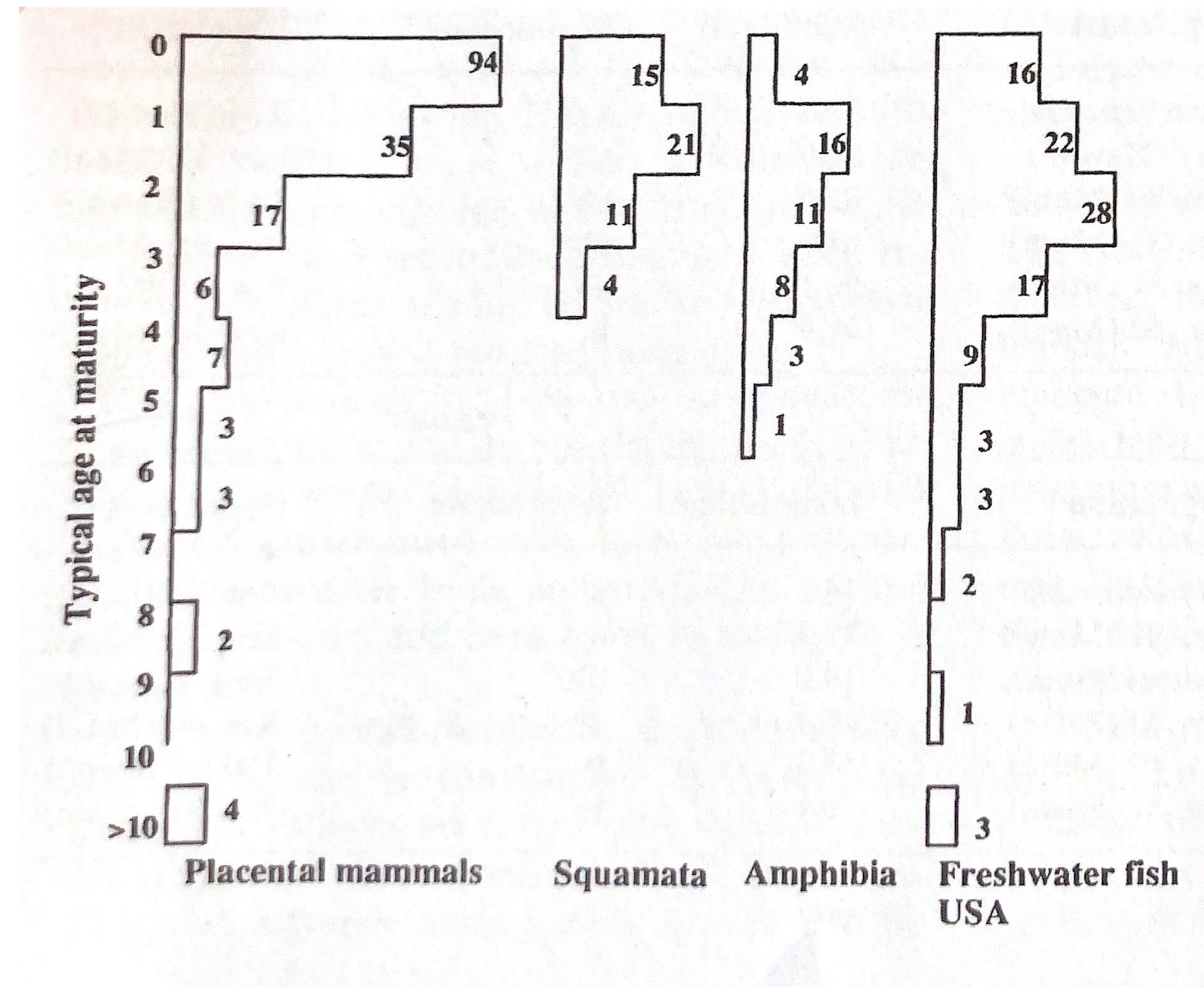
- **Iteroparity:** Reproduce multiple times





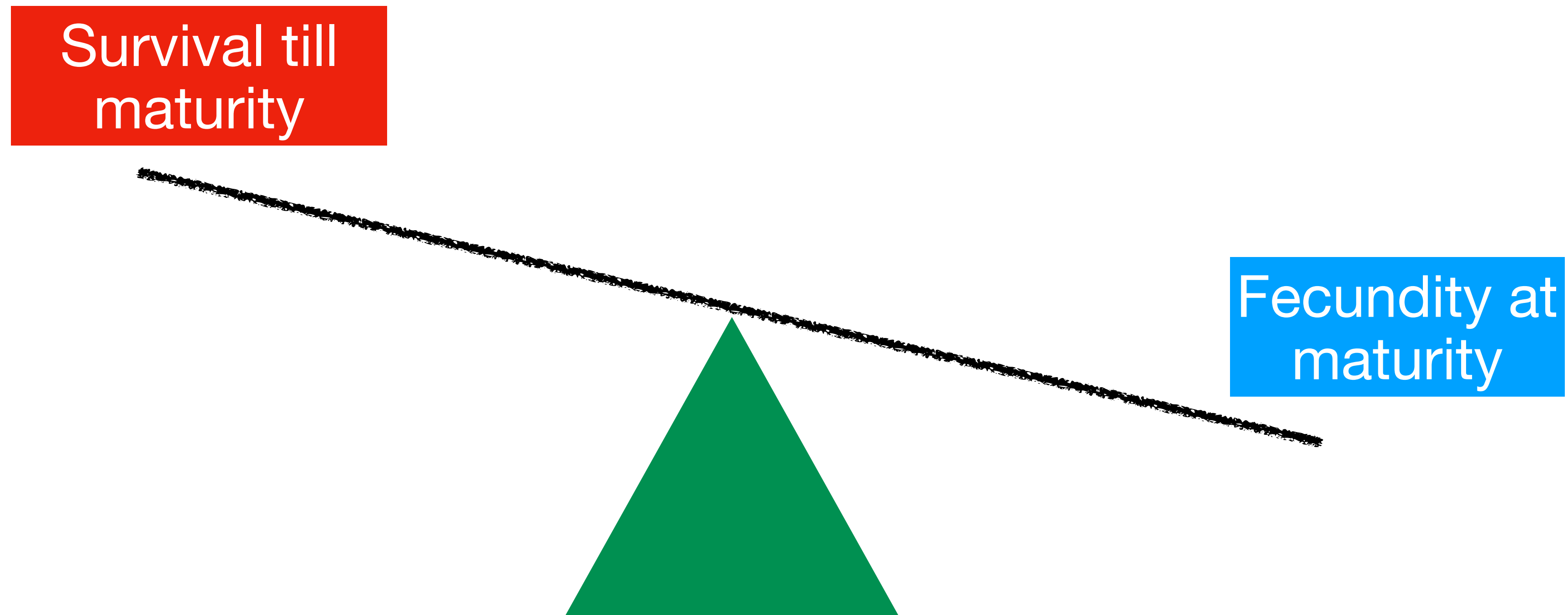
# Age at maturity

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



Bell (1980) Am Nat  
Stearns (1992)

# Age at maturity





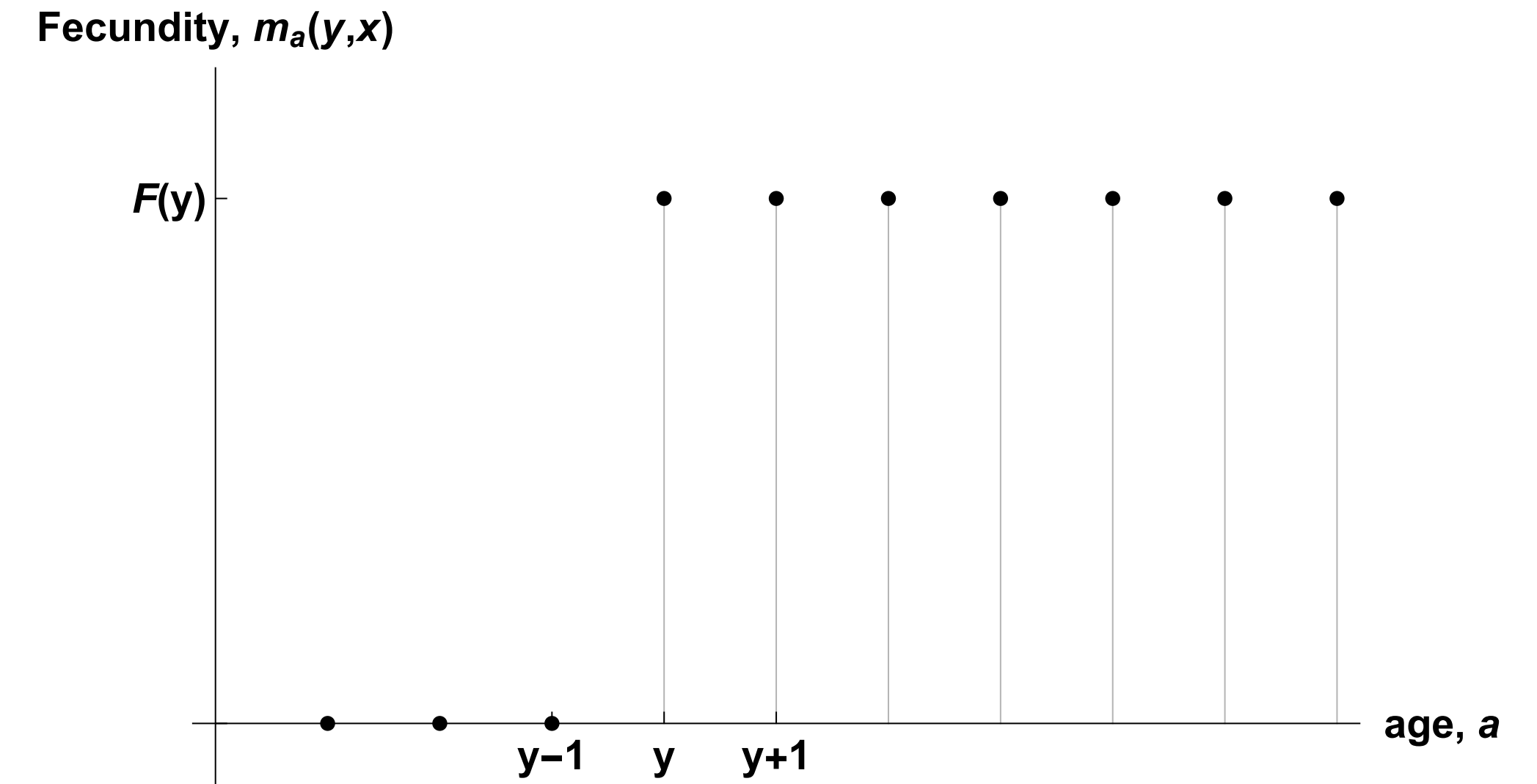
# Age at maturity

## A model

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

$$m_a(y, x) = \begin{cases} 0, & 1 \leq a < y \\ F(y), & y \leq a \end{cases}$$

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



# Age at maturity

## A model

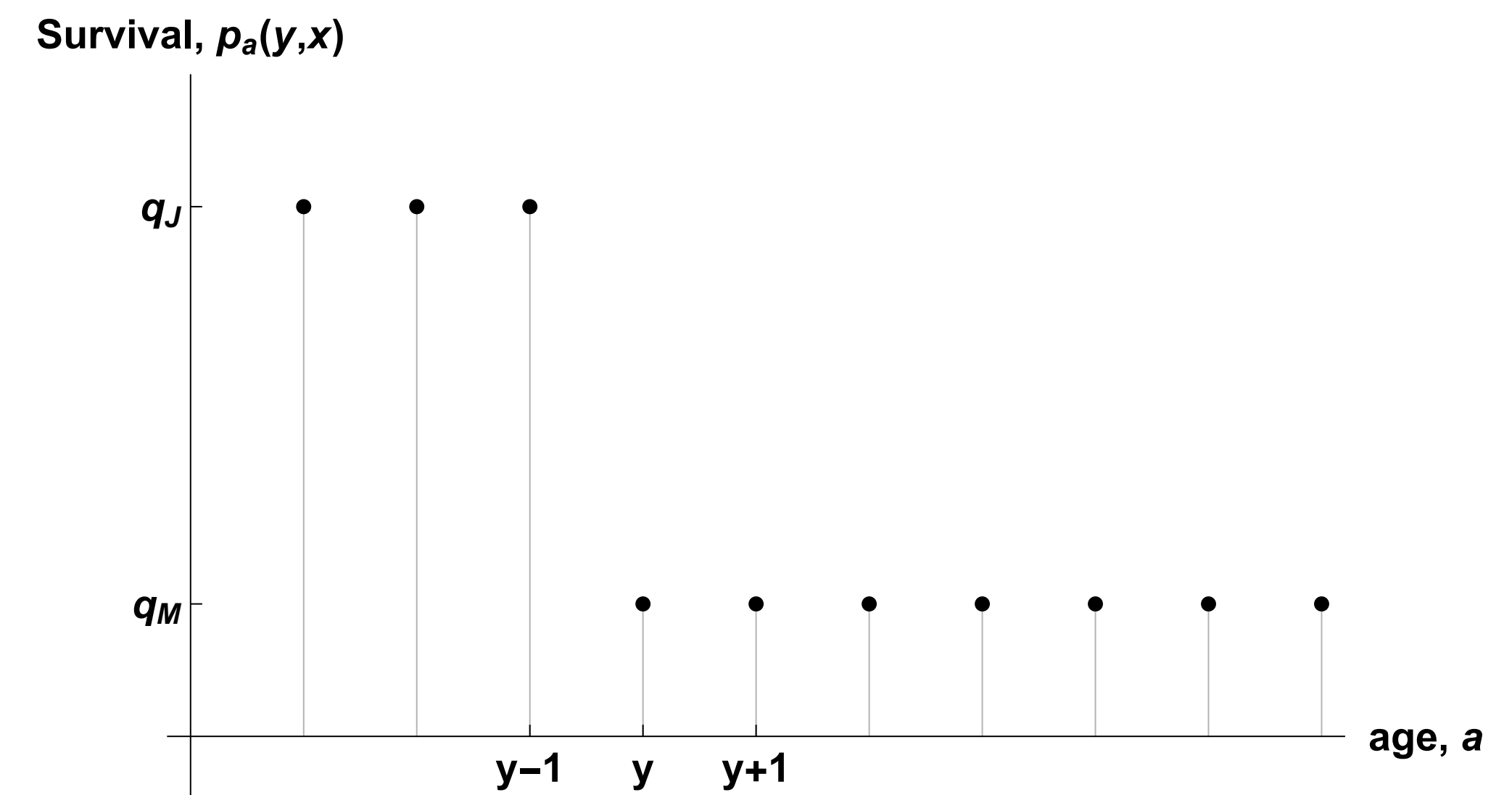
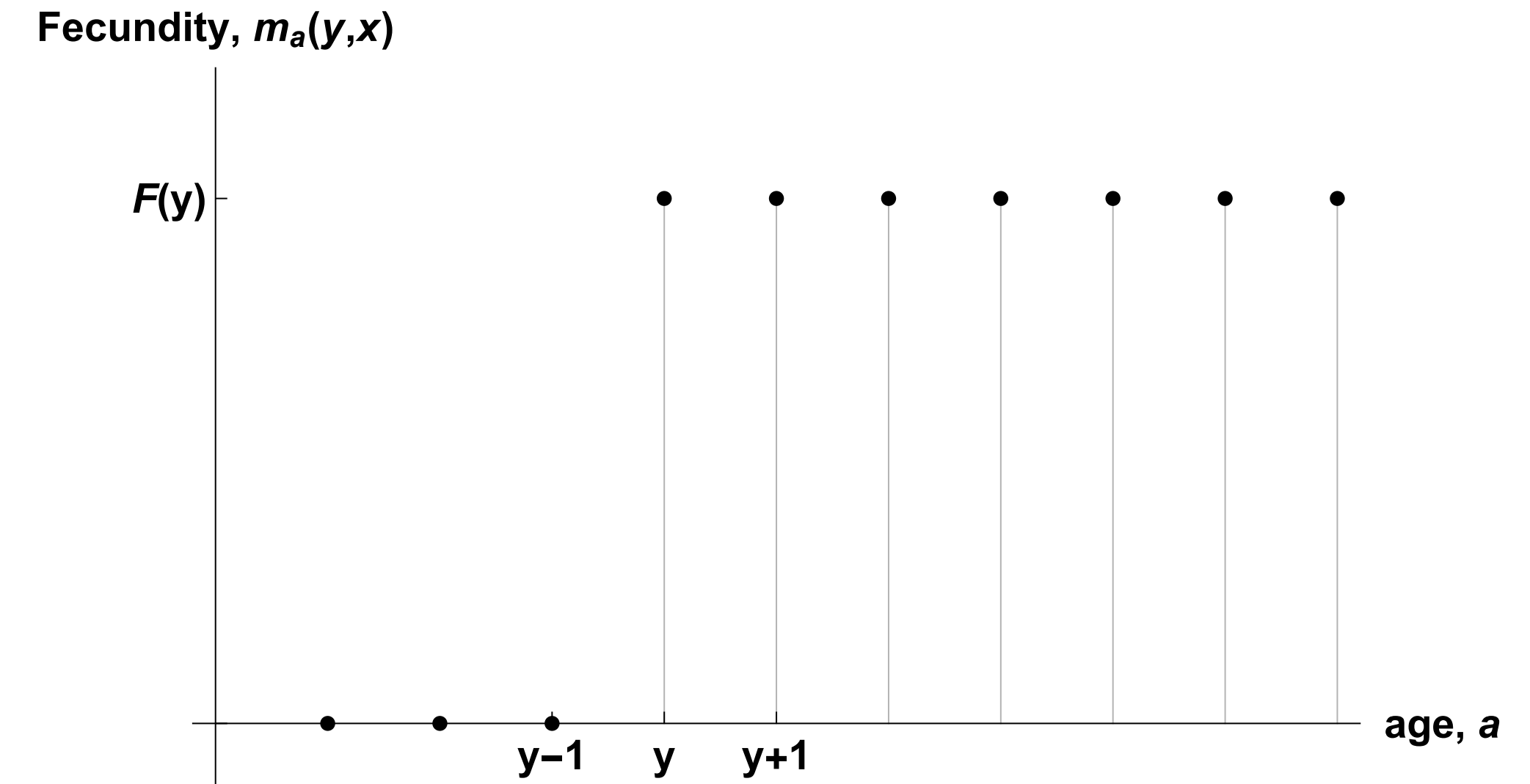
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**When is it advantageous to delay maturity by a year?**

# When is it advantageous to delay maturity by a year?

$$\text{When } R_0(x+1, x) = q_J \frac{F(x+1)}{F(x)} > 1, \text{ i.e. when } \frac{F(x)}{F(x+1)} < q_J$$

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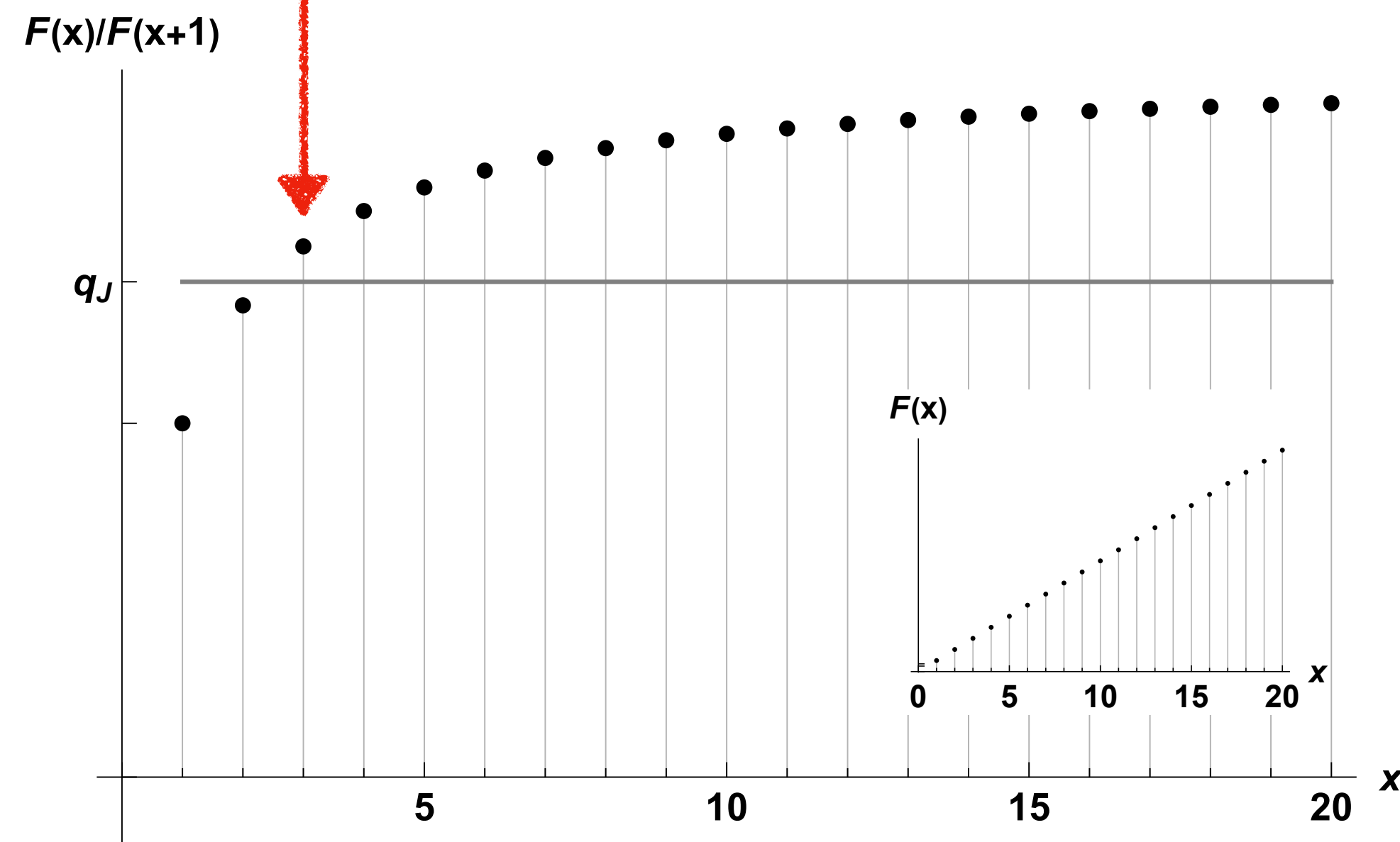
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optimal age = 3

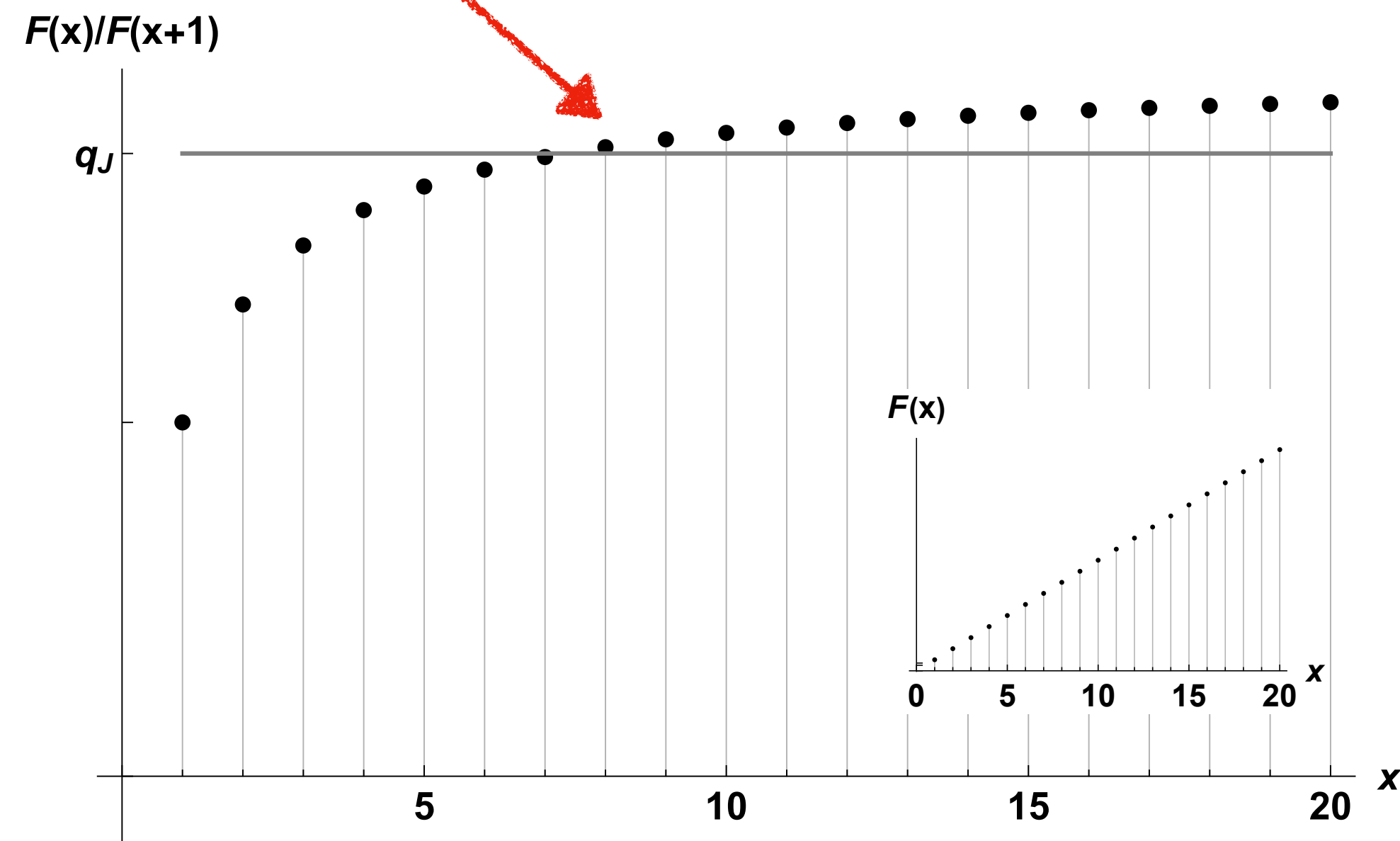


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When juvenile survival is high and/or fecundity increases quickly with age at maturity.

optimal age = 8

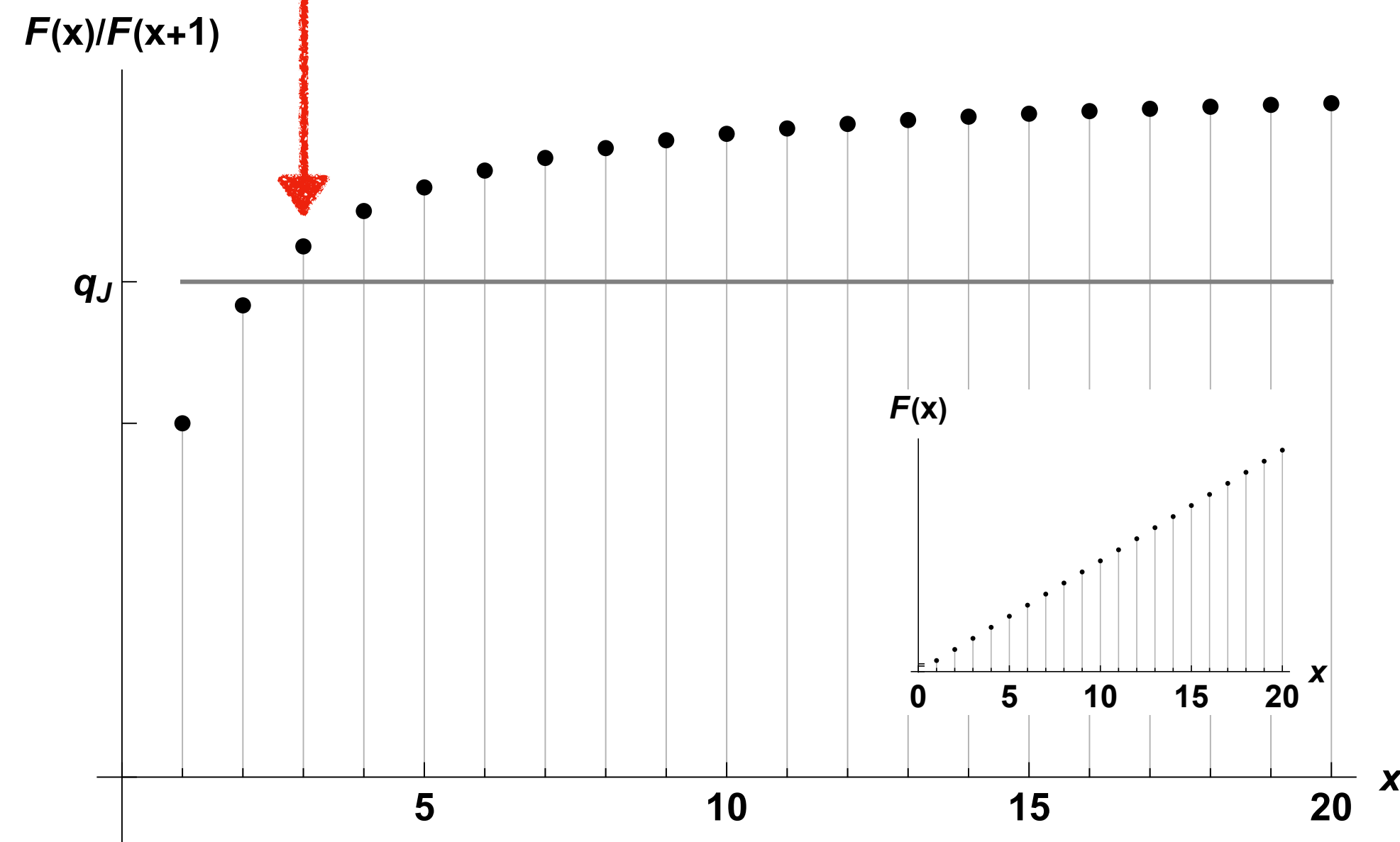


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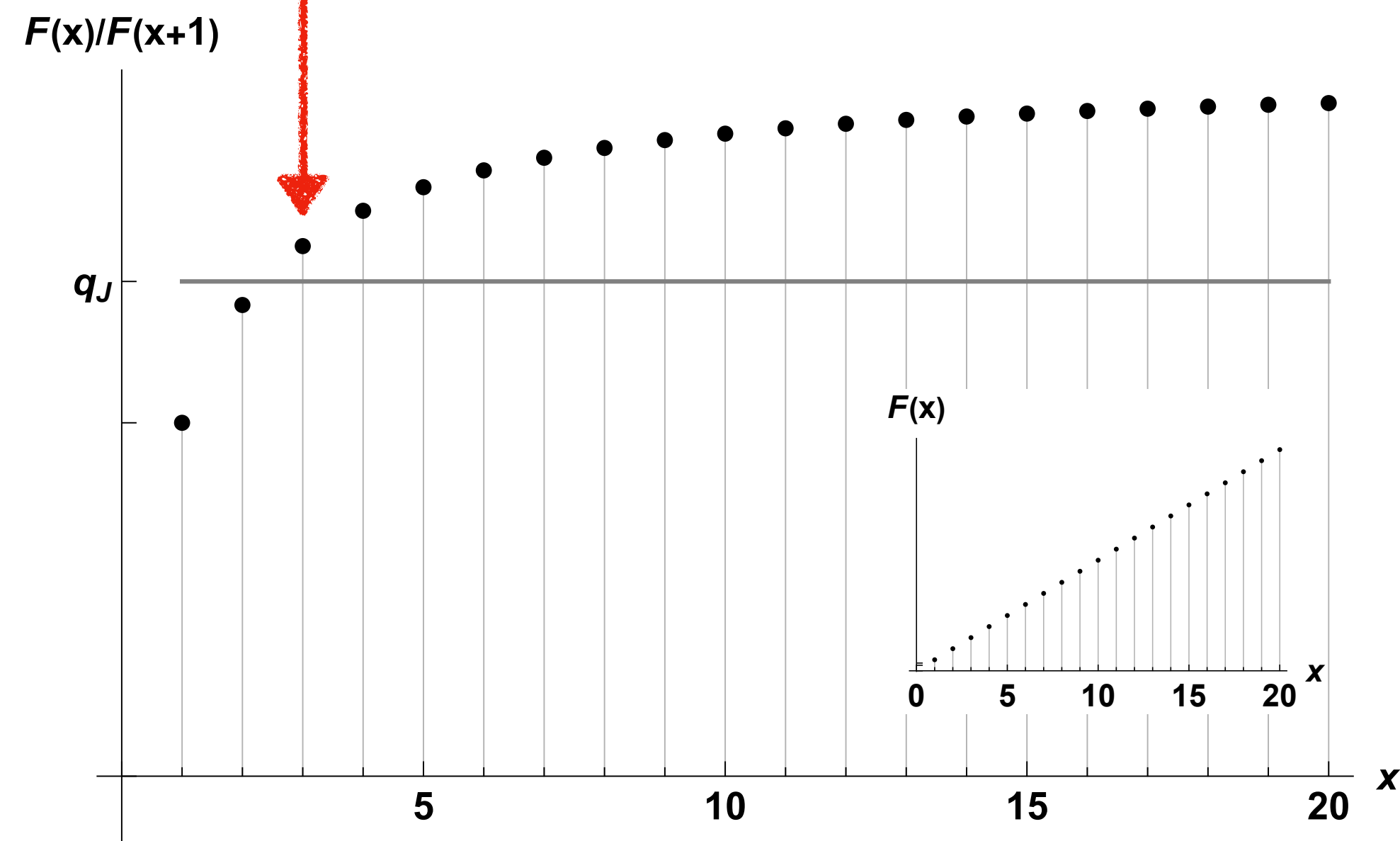


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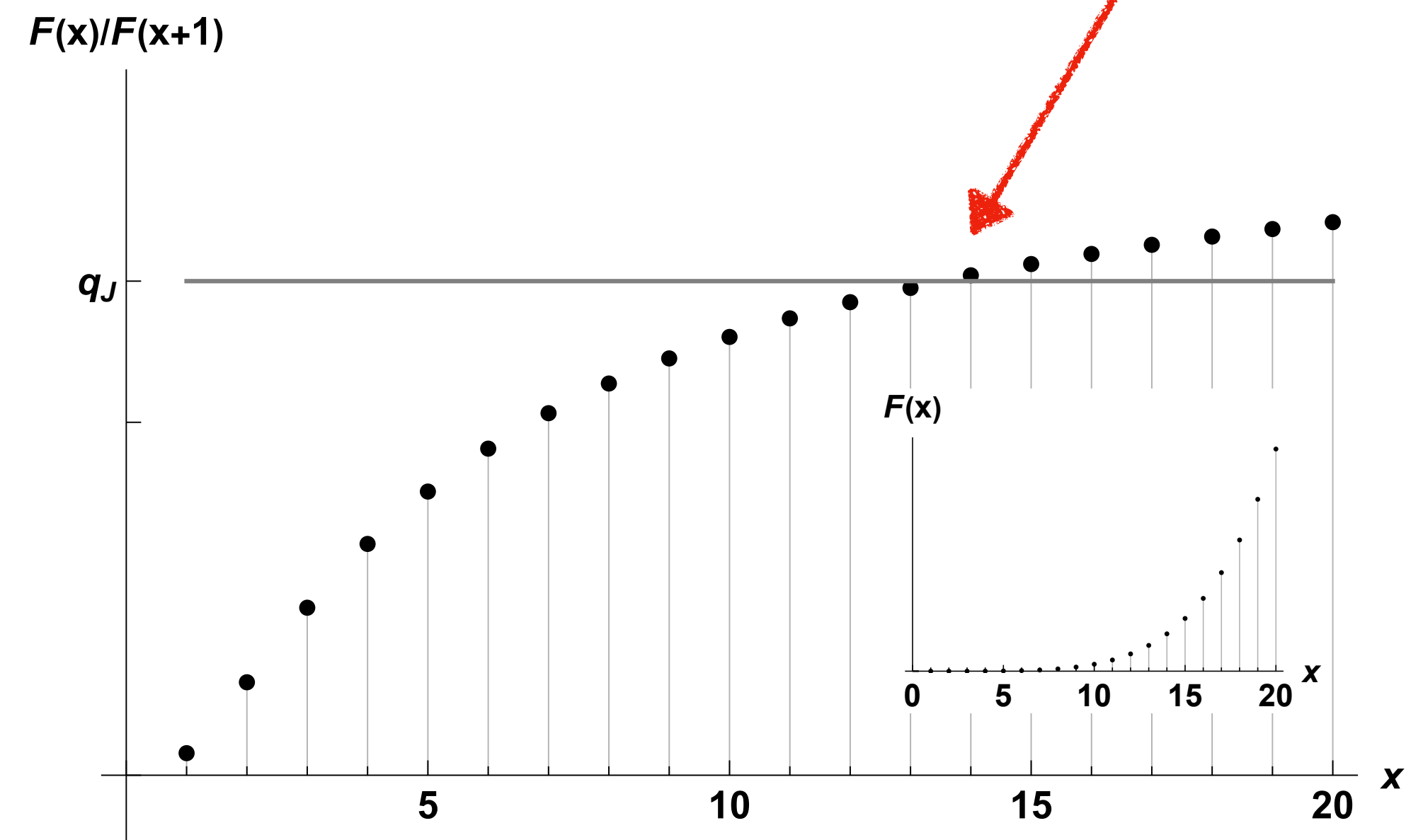
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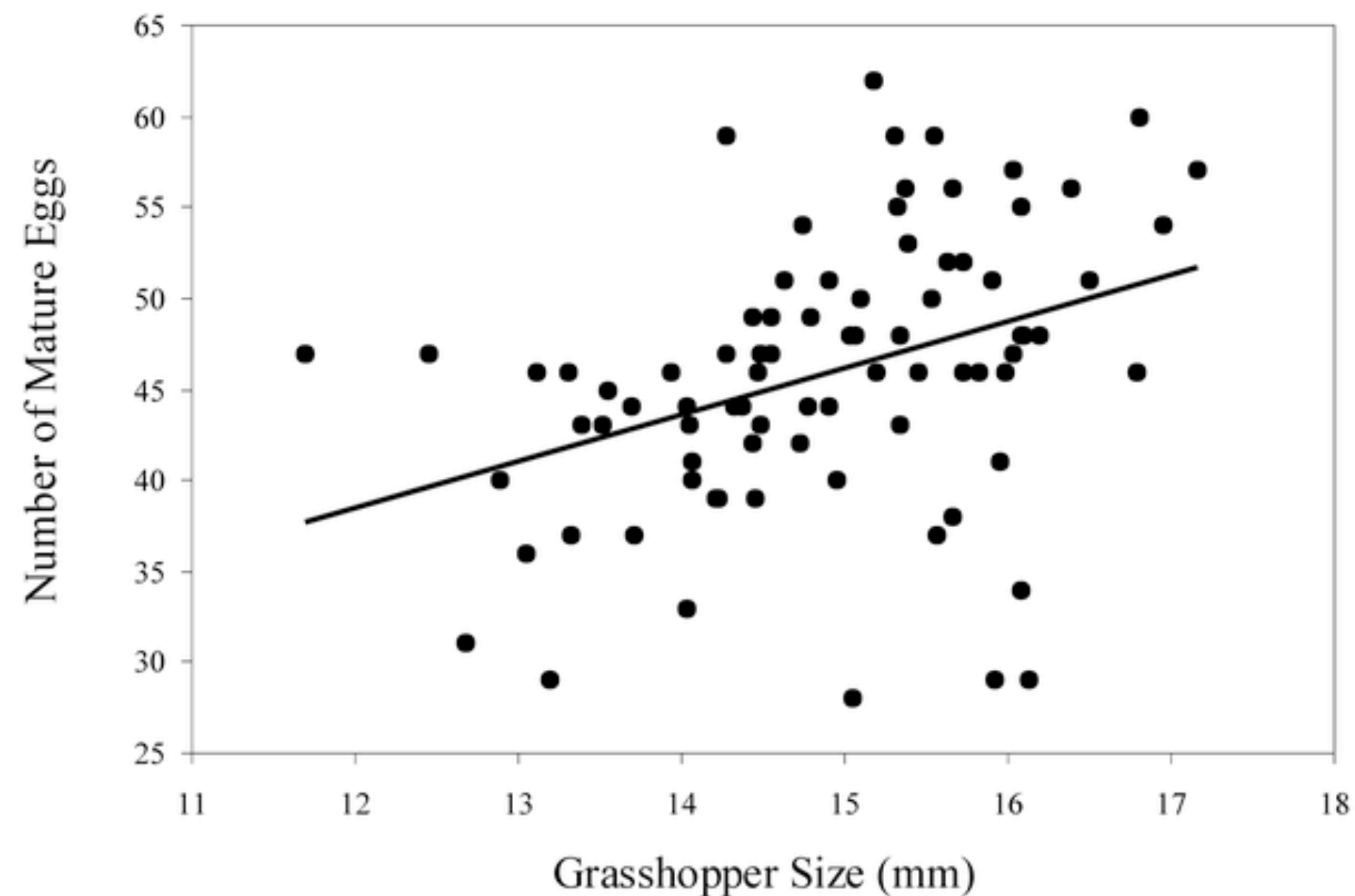


optimal age = 14



# Effect of size at maturity

Fecundity associated with size in many species

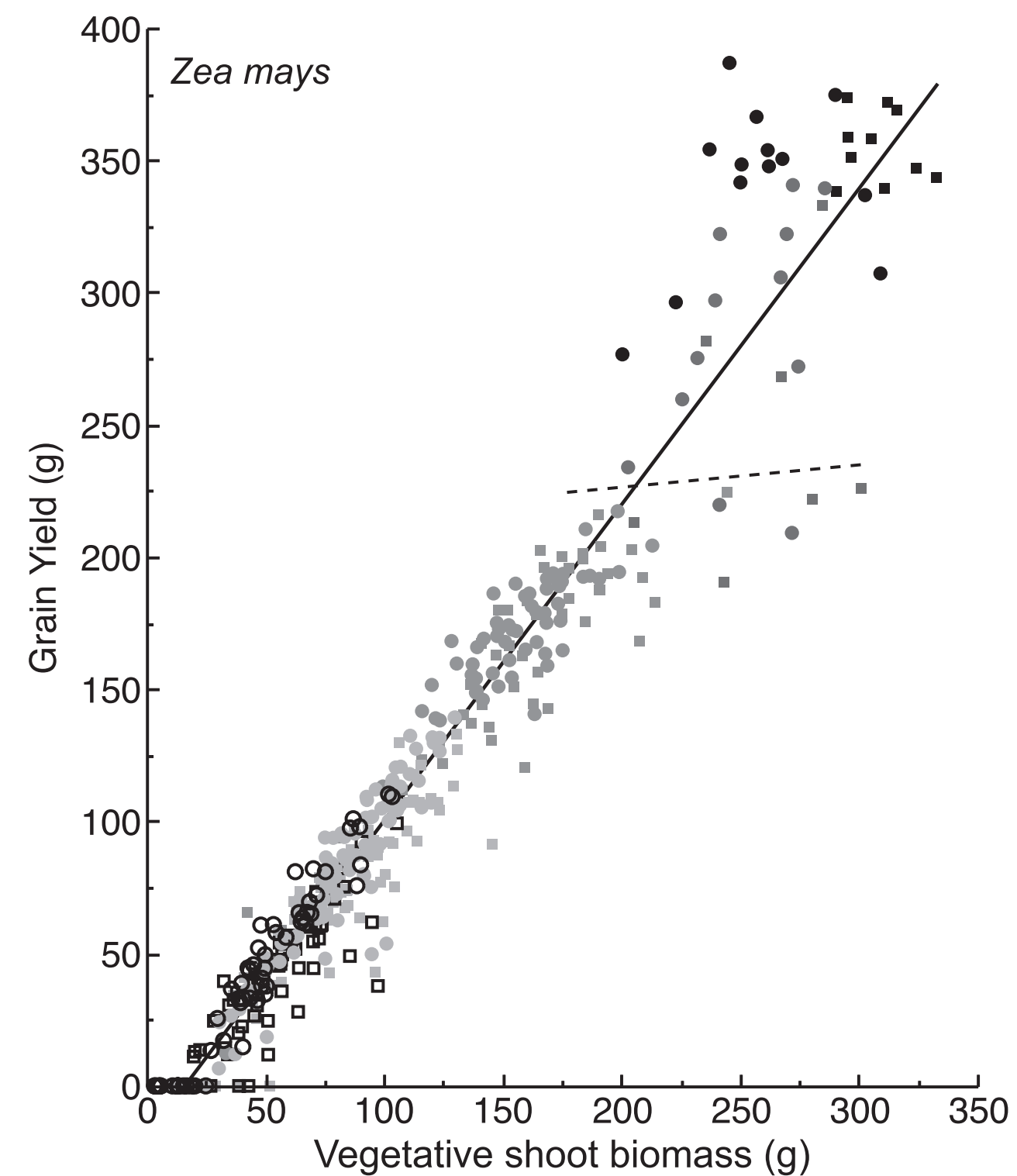


J. of Orthoptera Research, 17(2):265-271 (2008)

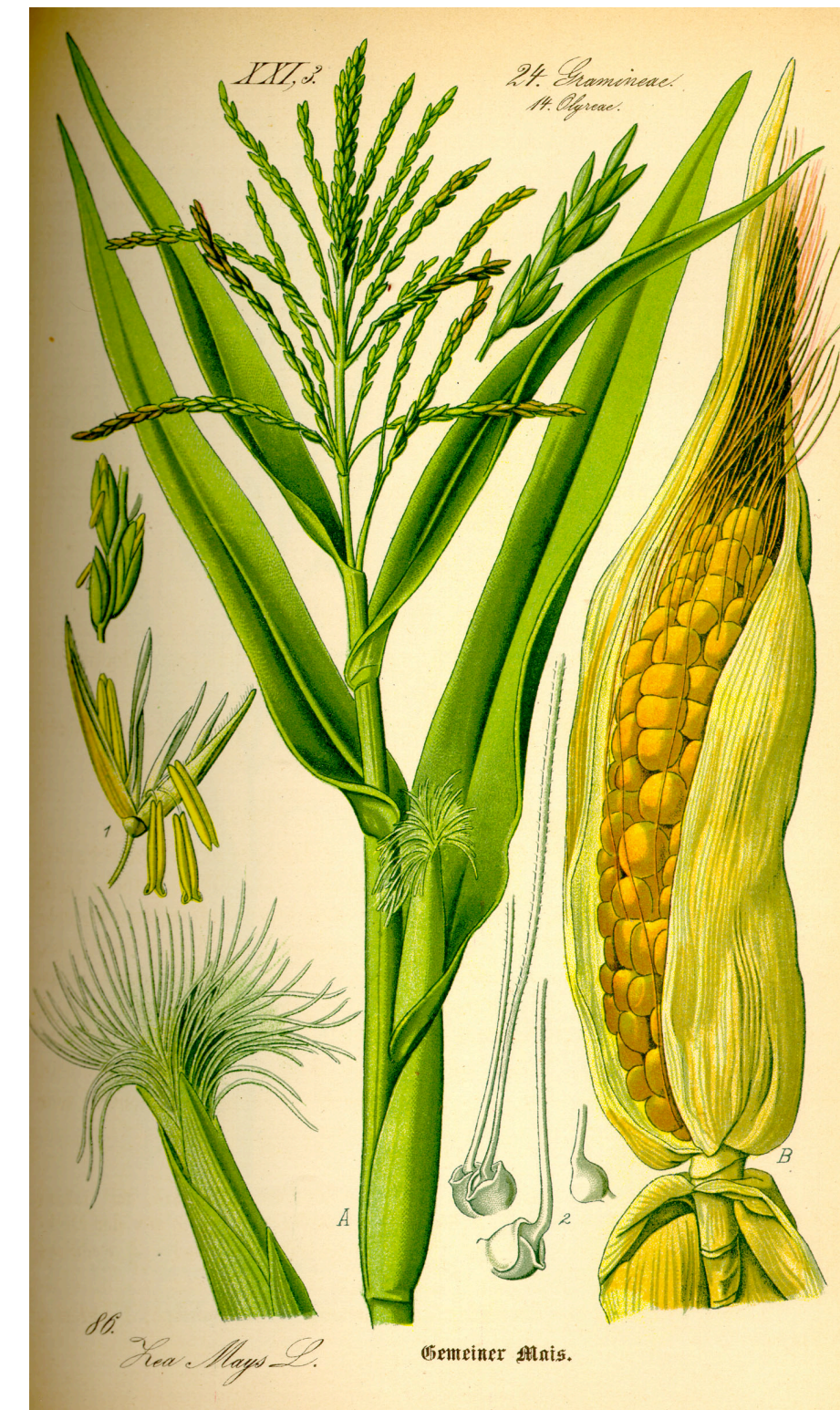


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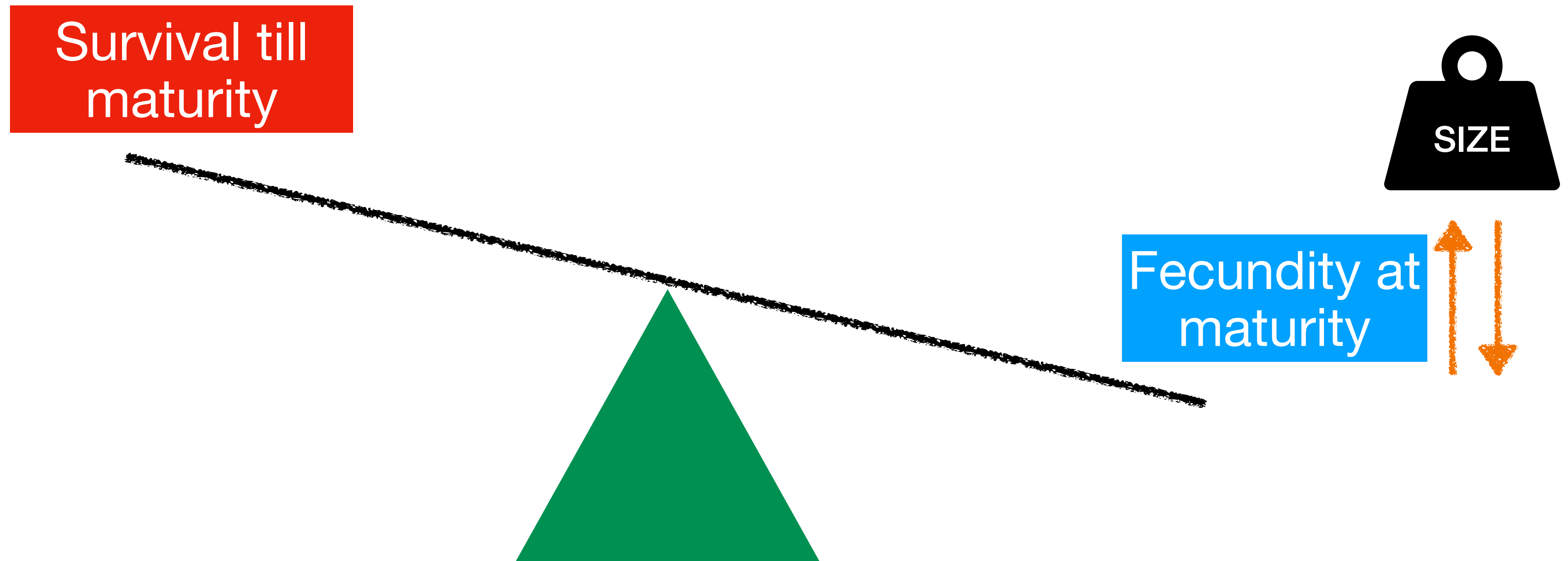


Weiner et al. Journal of Ecology 2009



# Effect of size at maturity

Mediates the survival/fecundity trade-off



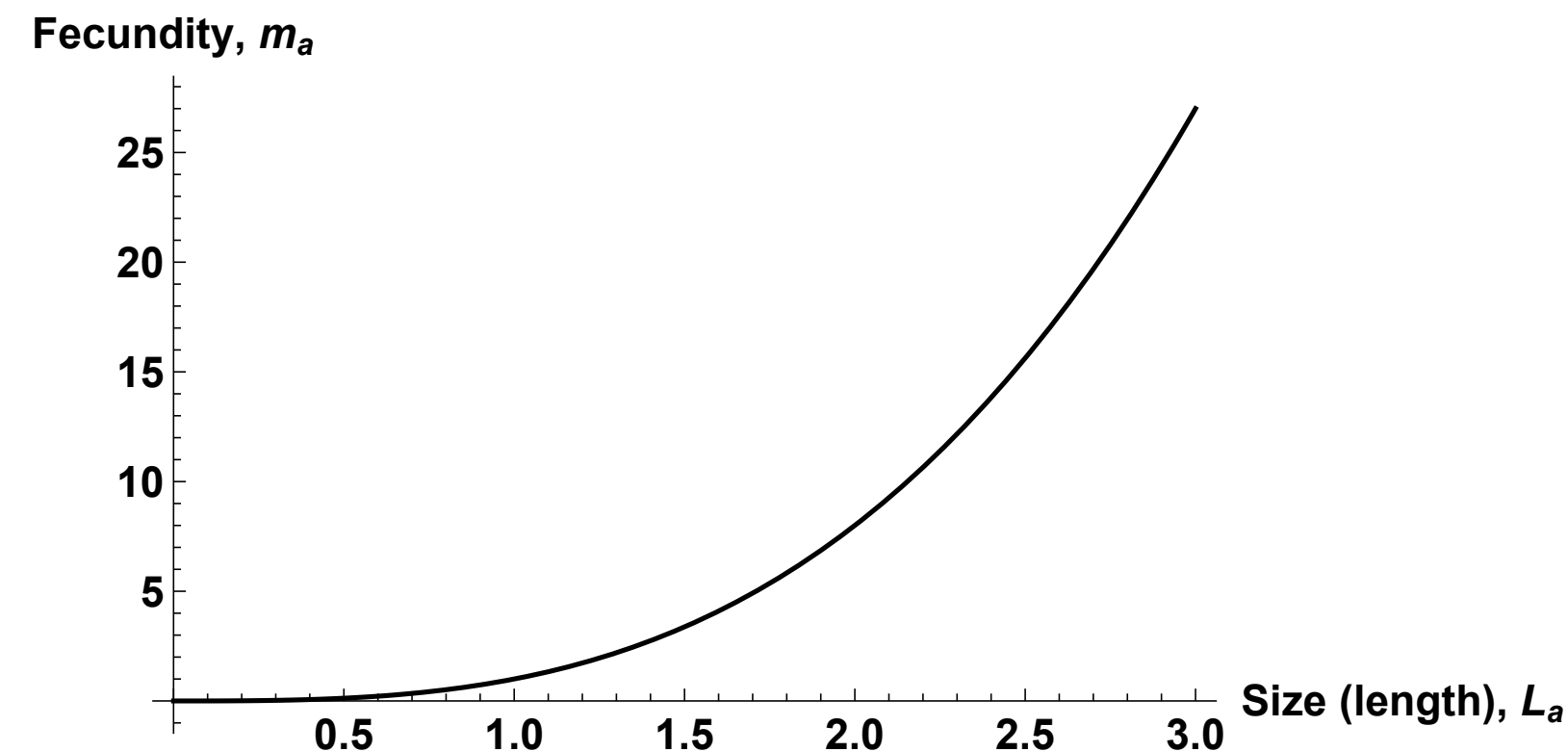
# Effect of size at maturity

## Roff's model (adapted)

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

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

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



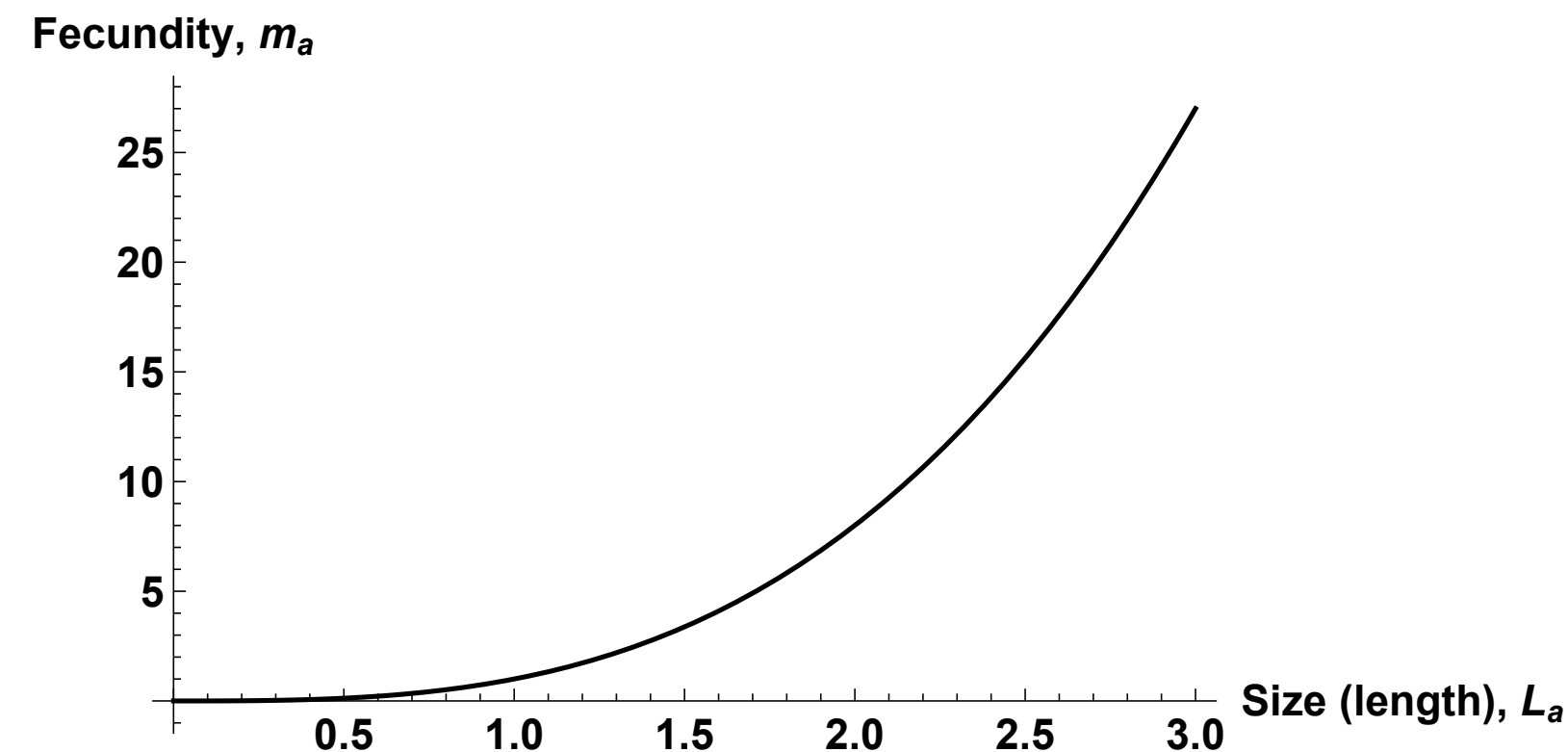
# Von Bertalanffy growth equations

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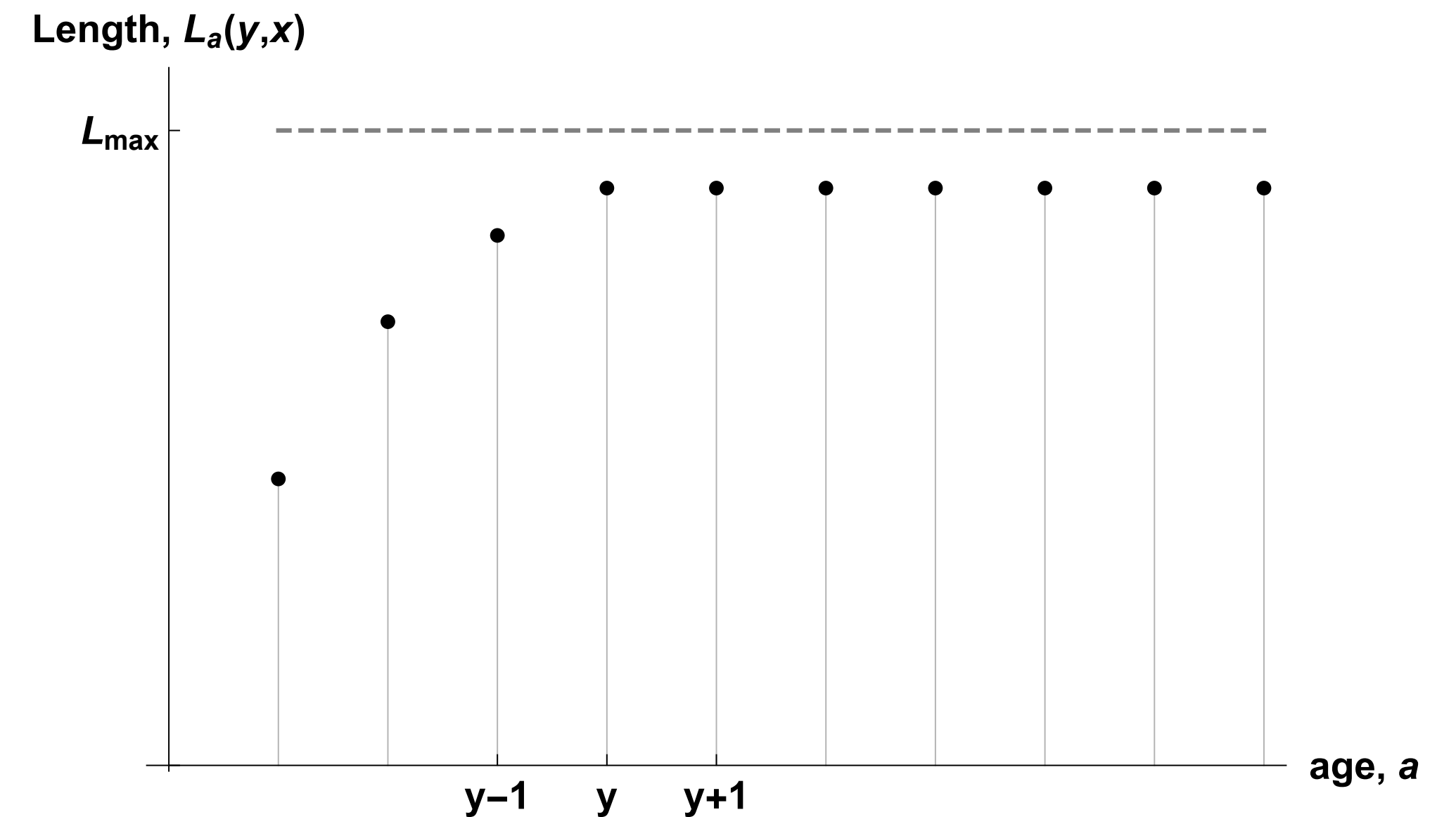
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$$L_a(y) = \begin{cases} L_{\max}(1 - e^{-ka}), & 1 \leq a < y \\ L_{\max}(1 - e^{-ky}), & y \leq a \end{cases}$$





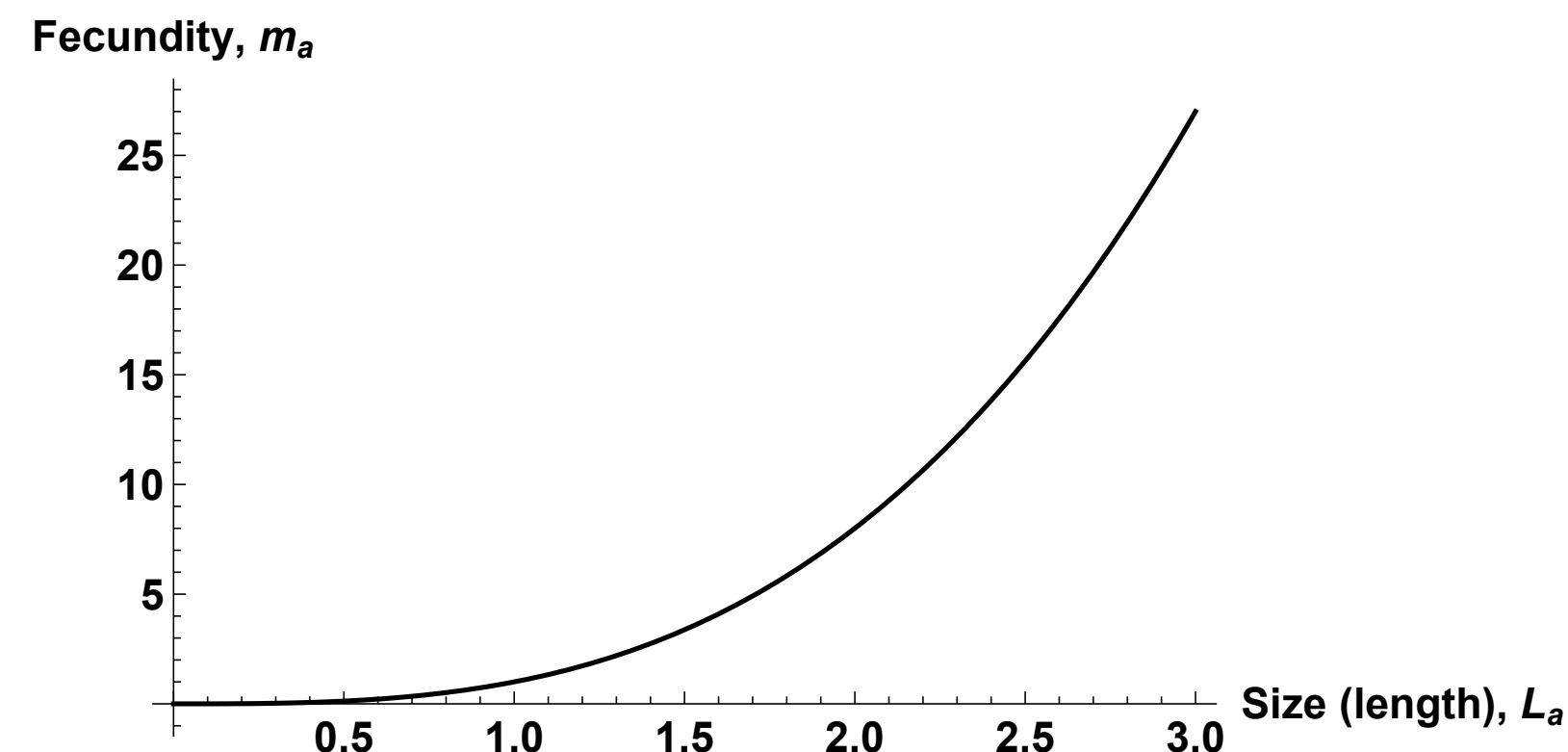
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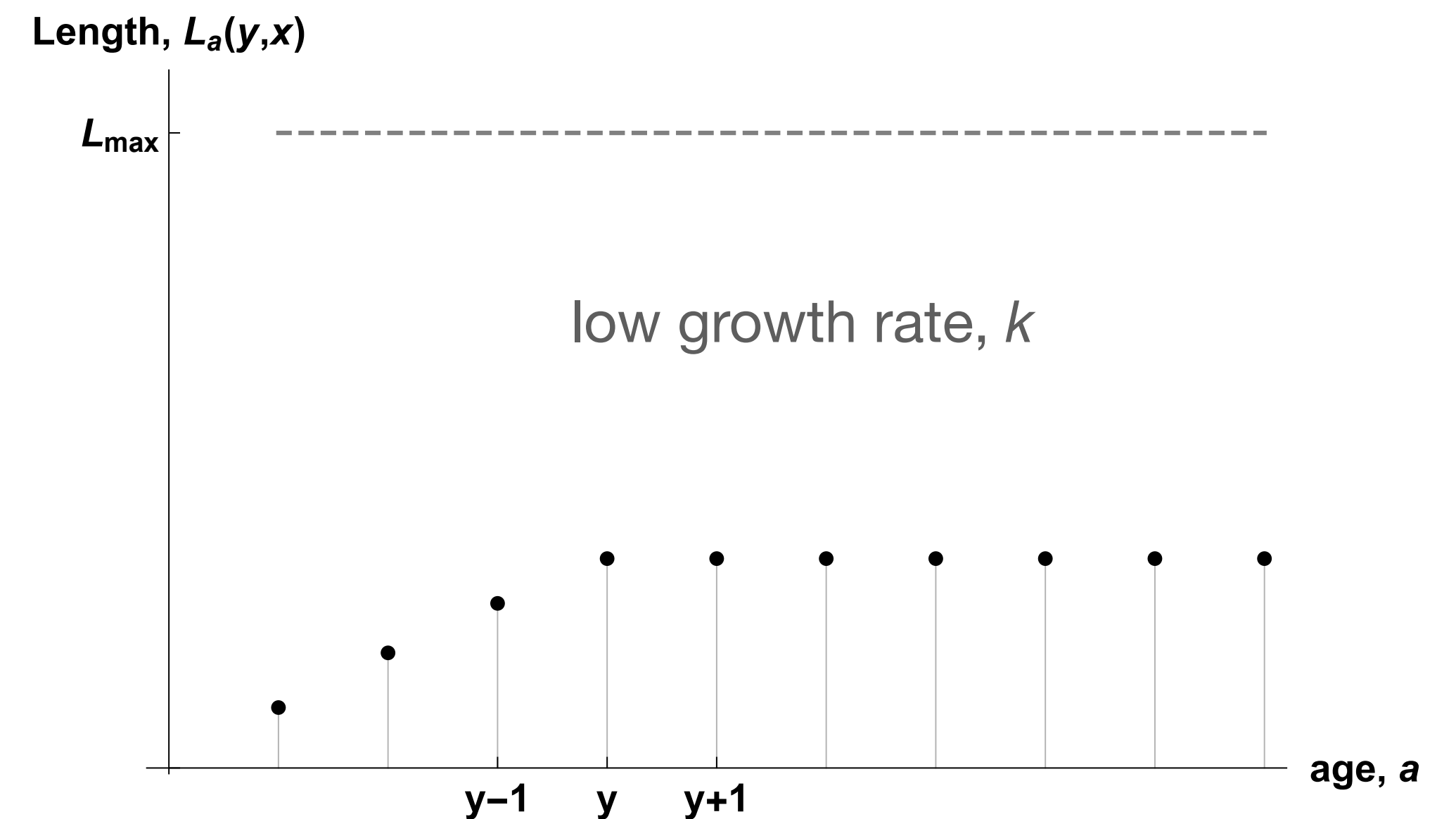
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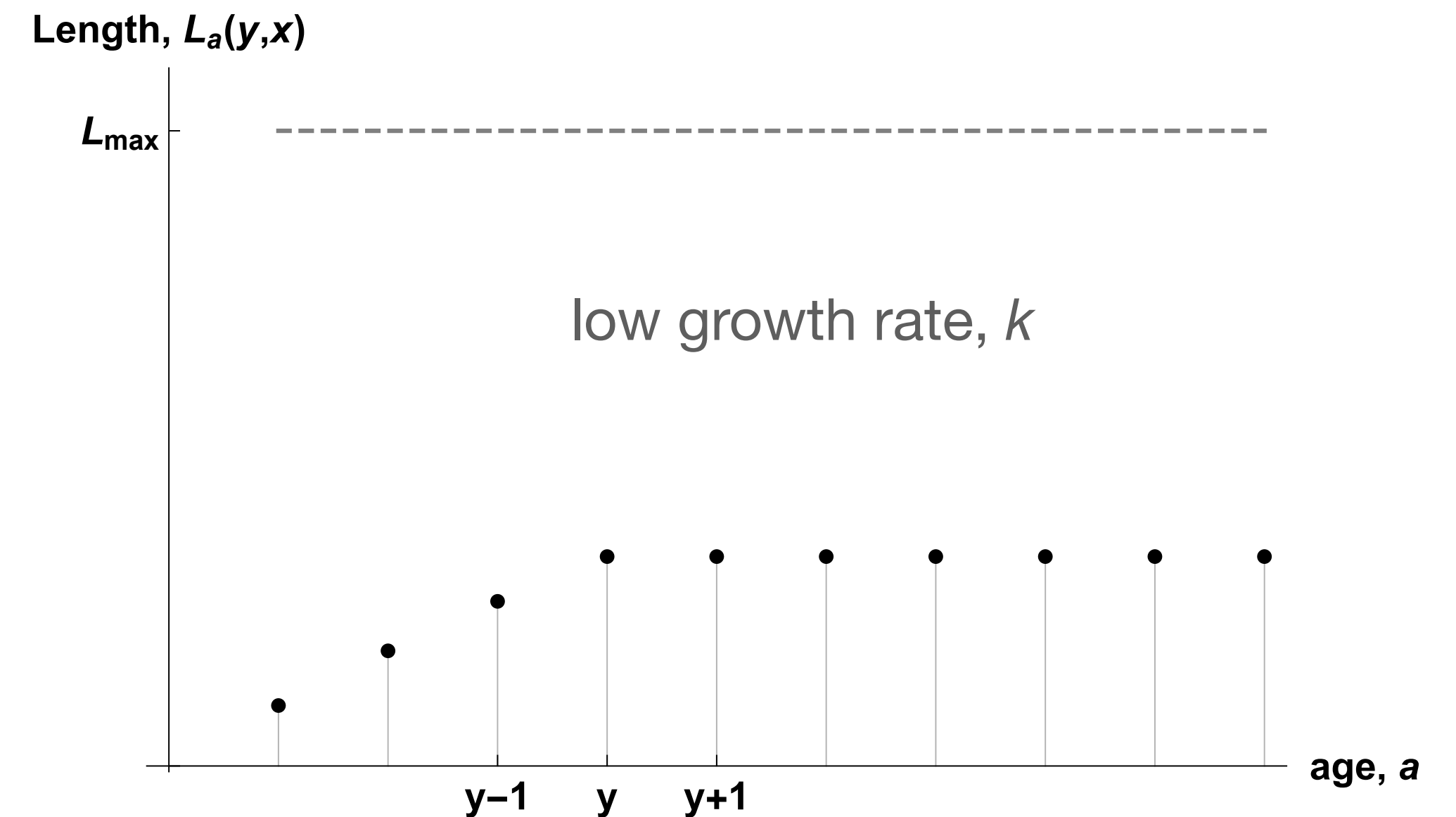
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# Mutant reproductive success

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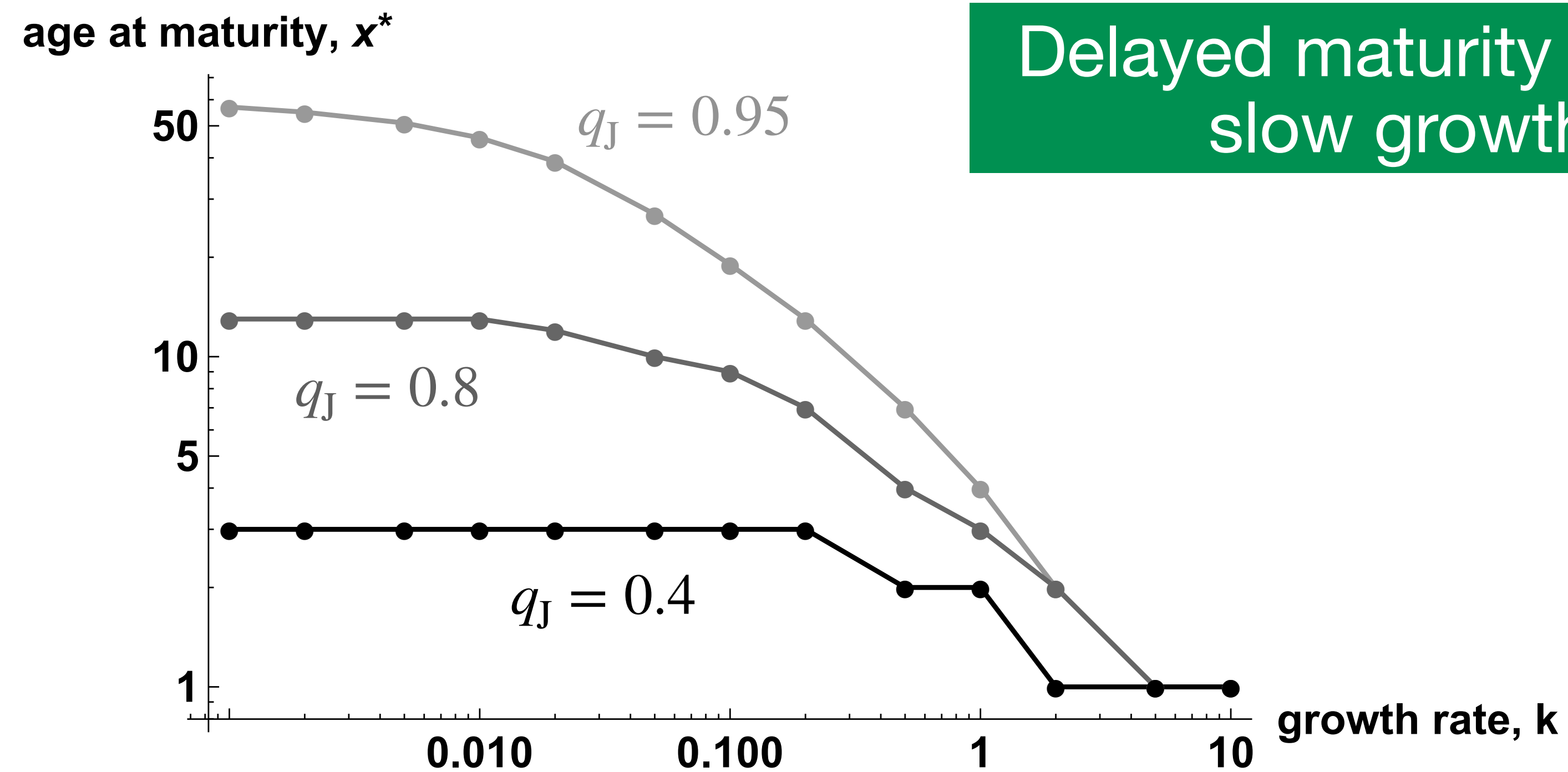
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# Optimal age at maturity

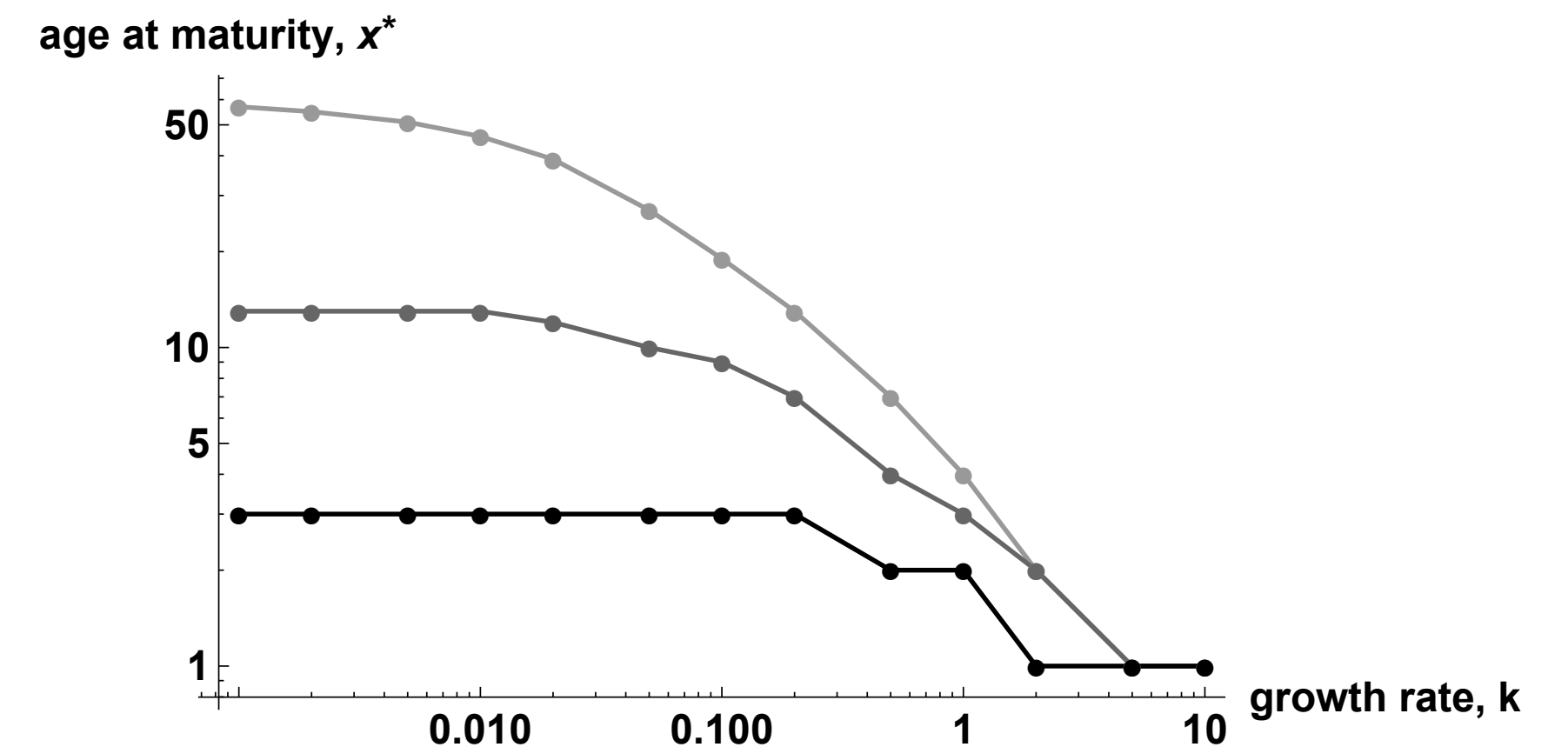
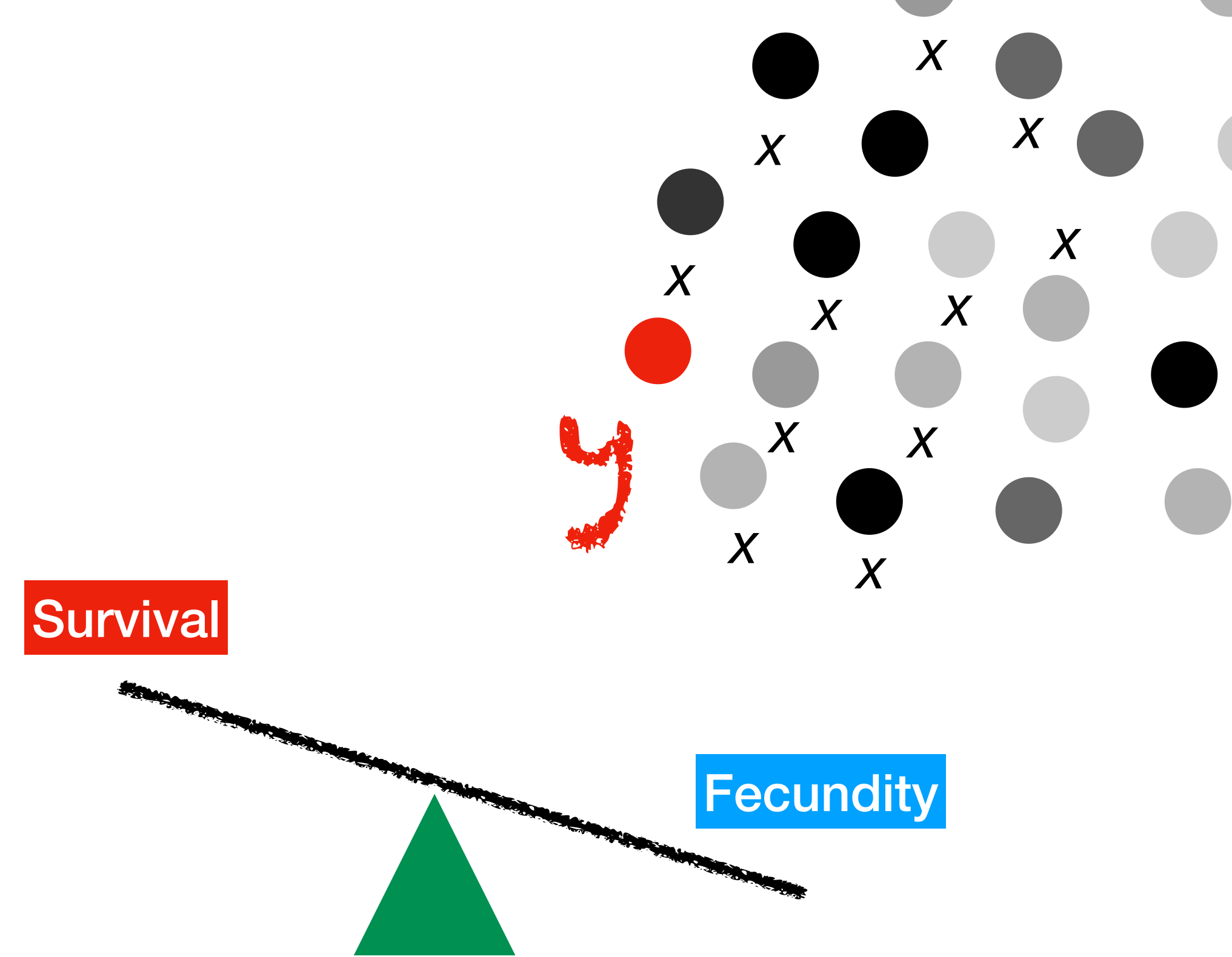


Delayed maturity favoured by slow growth rate.

# 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.

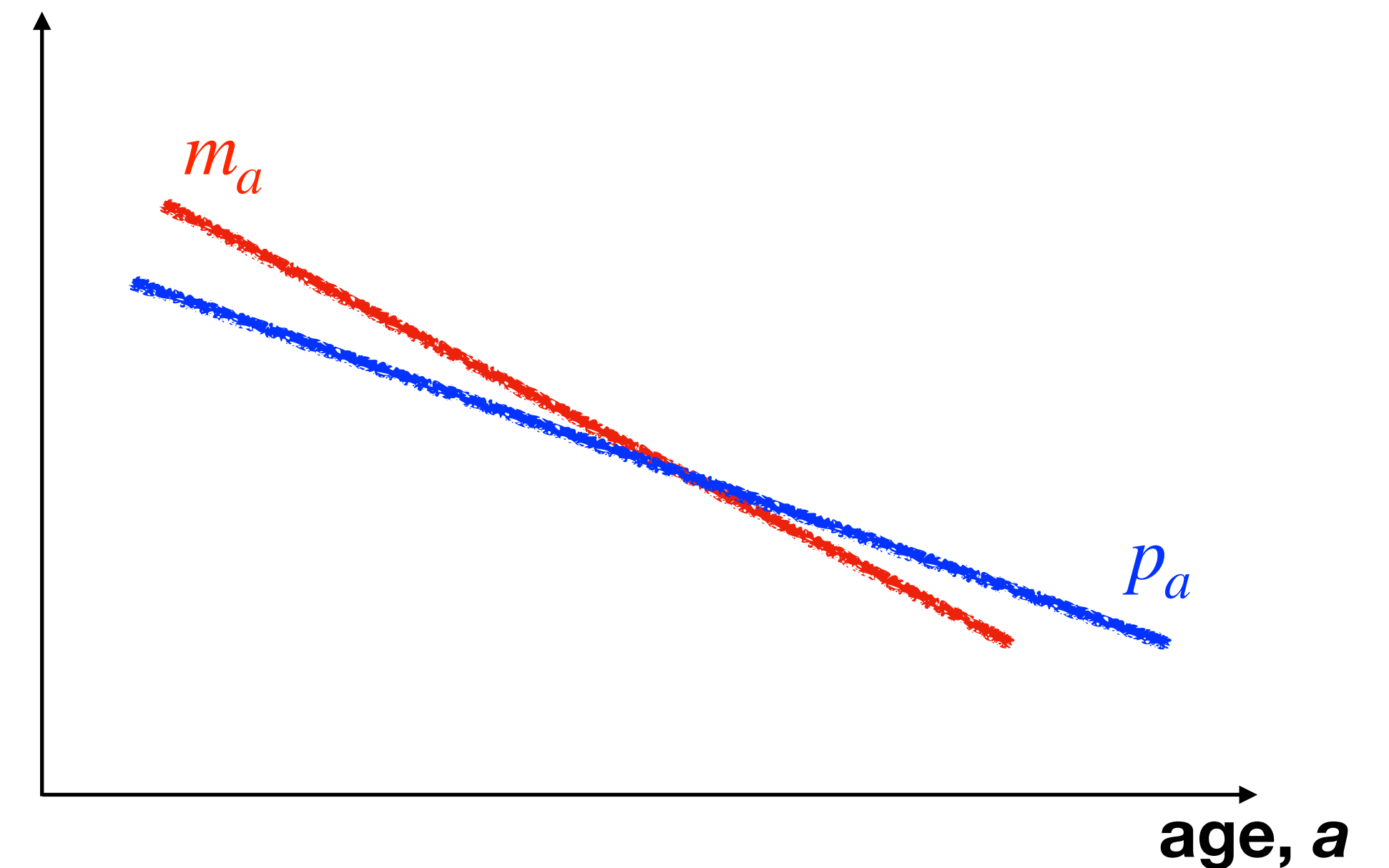
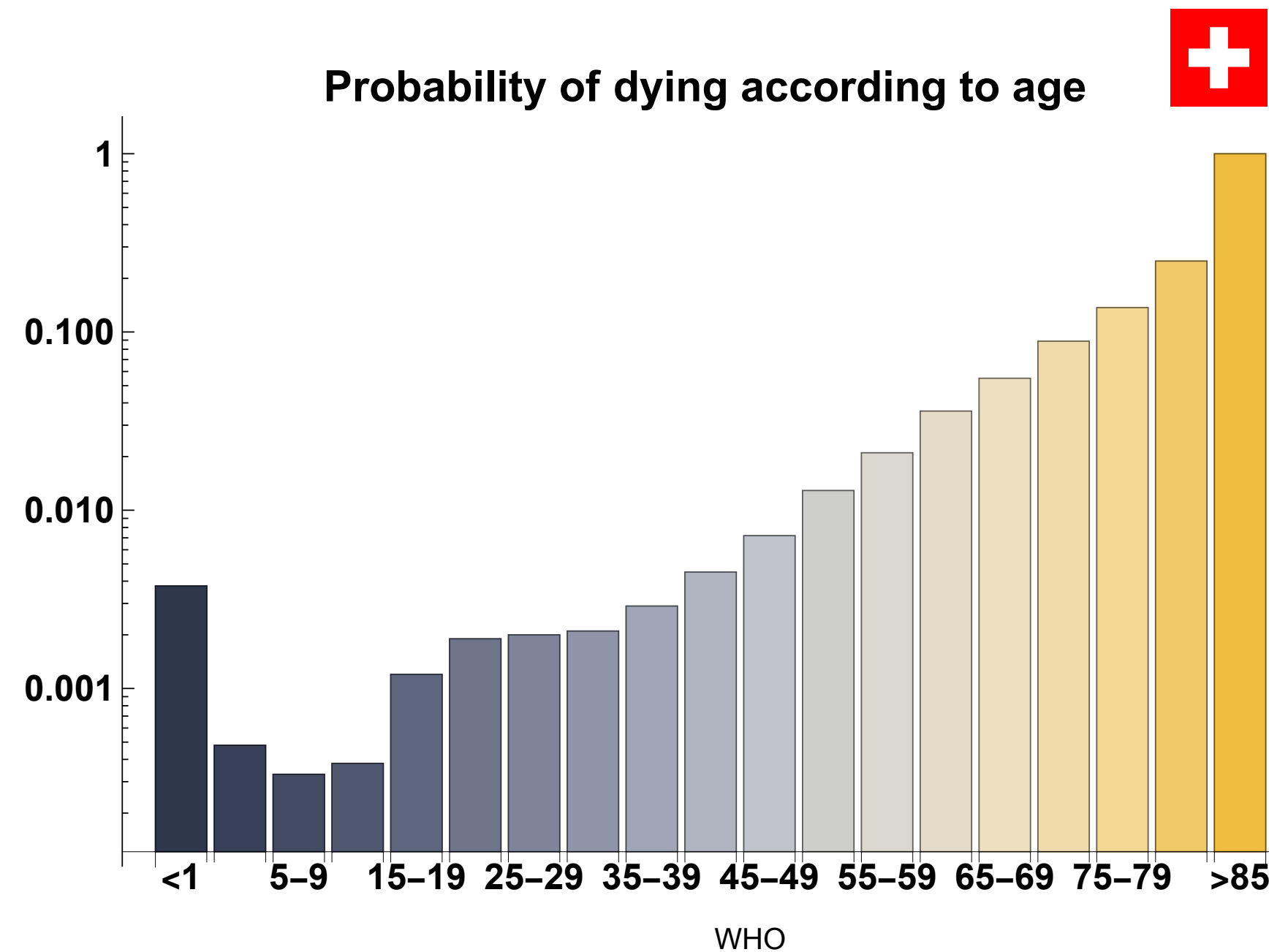


# Evolution of ageing



# Recap

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





# Strength of selection on age specific traits

Hamilton 1966

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

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

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



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**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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$$\begin{array}{ccccccc} \text{Survival} & & \text{Selection on} & & \text{Selection on} & & \text{Reproductive} \\ \text{till age} & & \text{fecundity at} & + & \text{survival} & \times & \text{value of age} \\ a & & \text{age } a & & \text{from age} & & a+1 \\ & & & & \text{a to a+1} & & \end{array} \left[ \right]$$

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Survival till age  $a$        $\left[ \begin{array}{l} \text{Selection on fecundity at age } a \\ + \\ \text{Selection on survival from age } a \text{ to } a+1 \end{array} \right] \times \text{Reproductive value of age } a+1$

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selection is  
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selection on  
survival  
proportional to  
reproductive value

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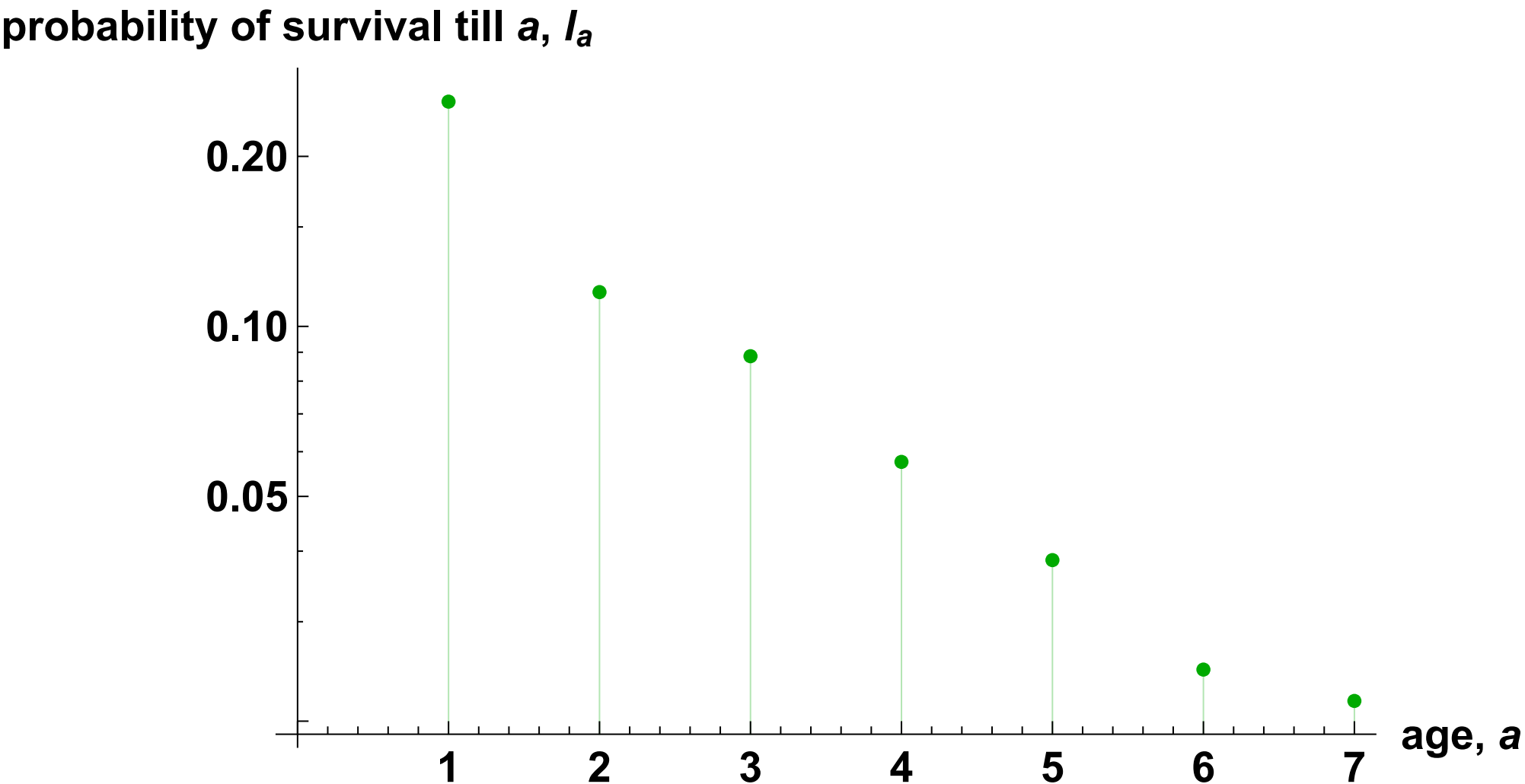
Gray squirrel example (with fecundity scaled so that  $R_0 = 1$ )

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
5	0.64	2.05	0.57
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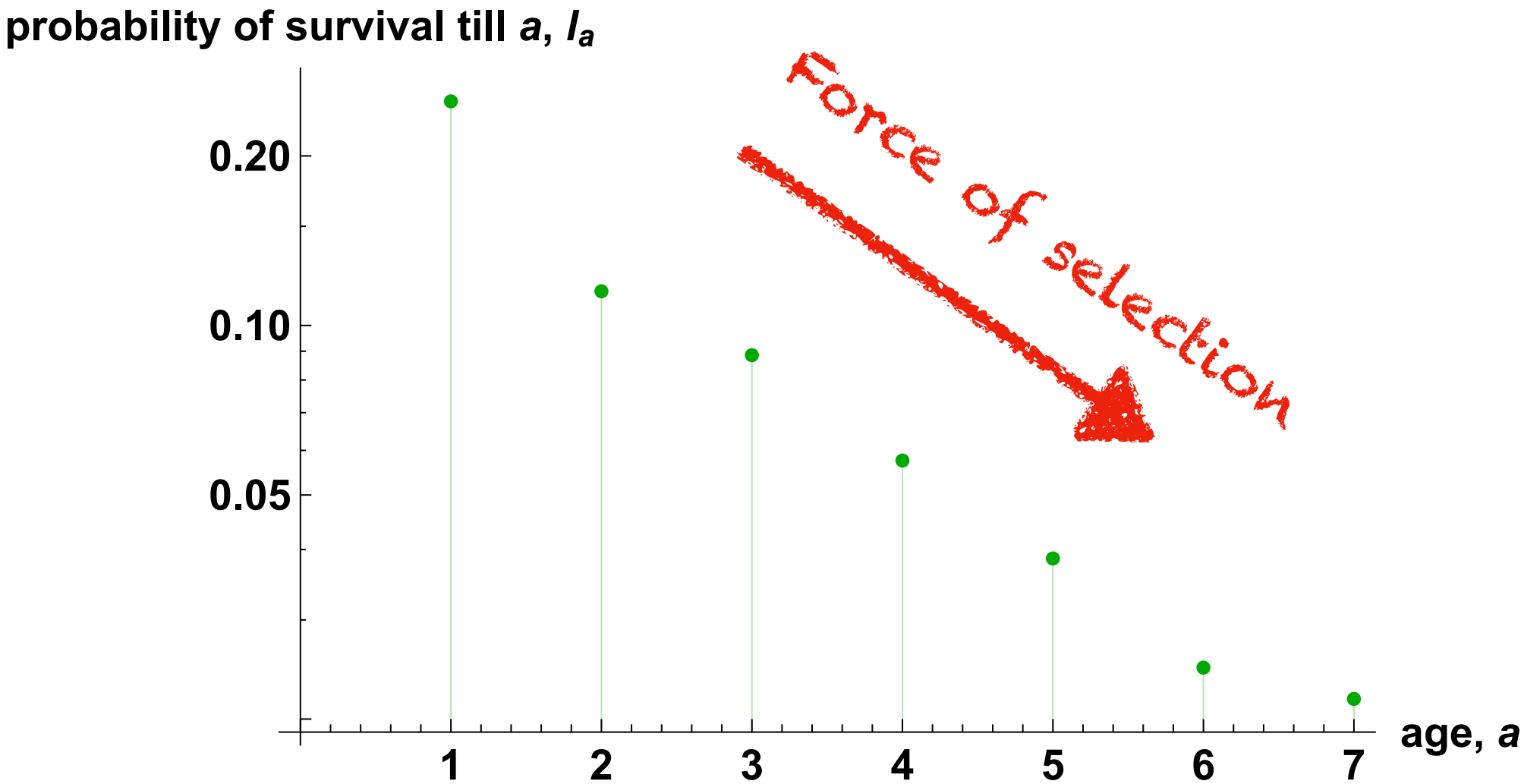
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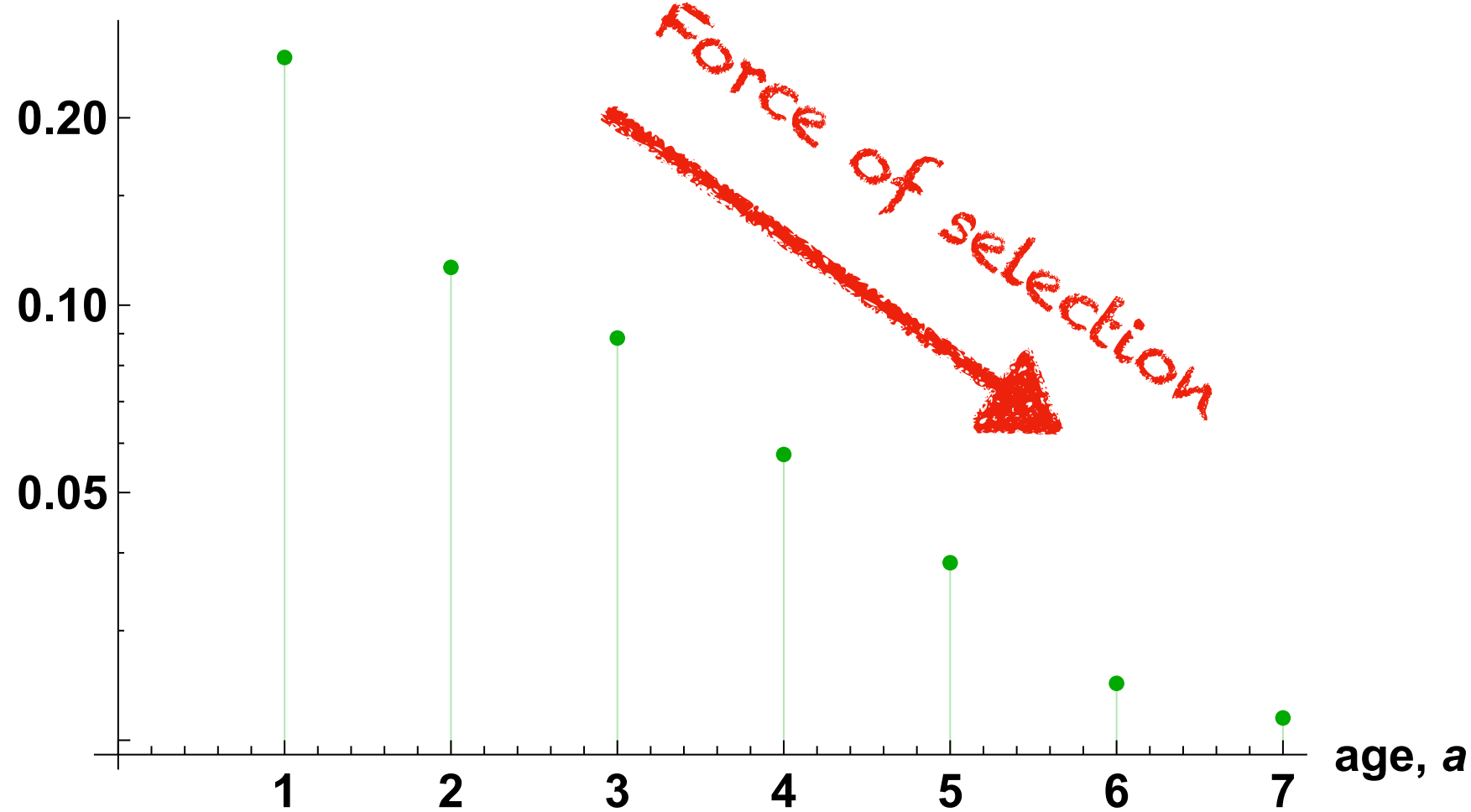
selection on fecundity decreases with age

# Strength of selection decreases with age

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

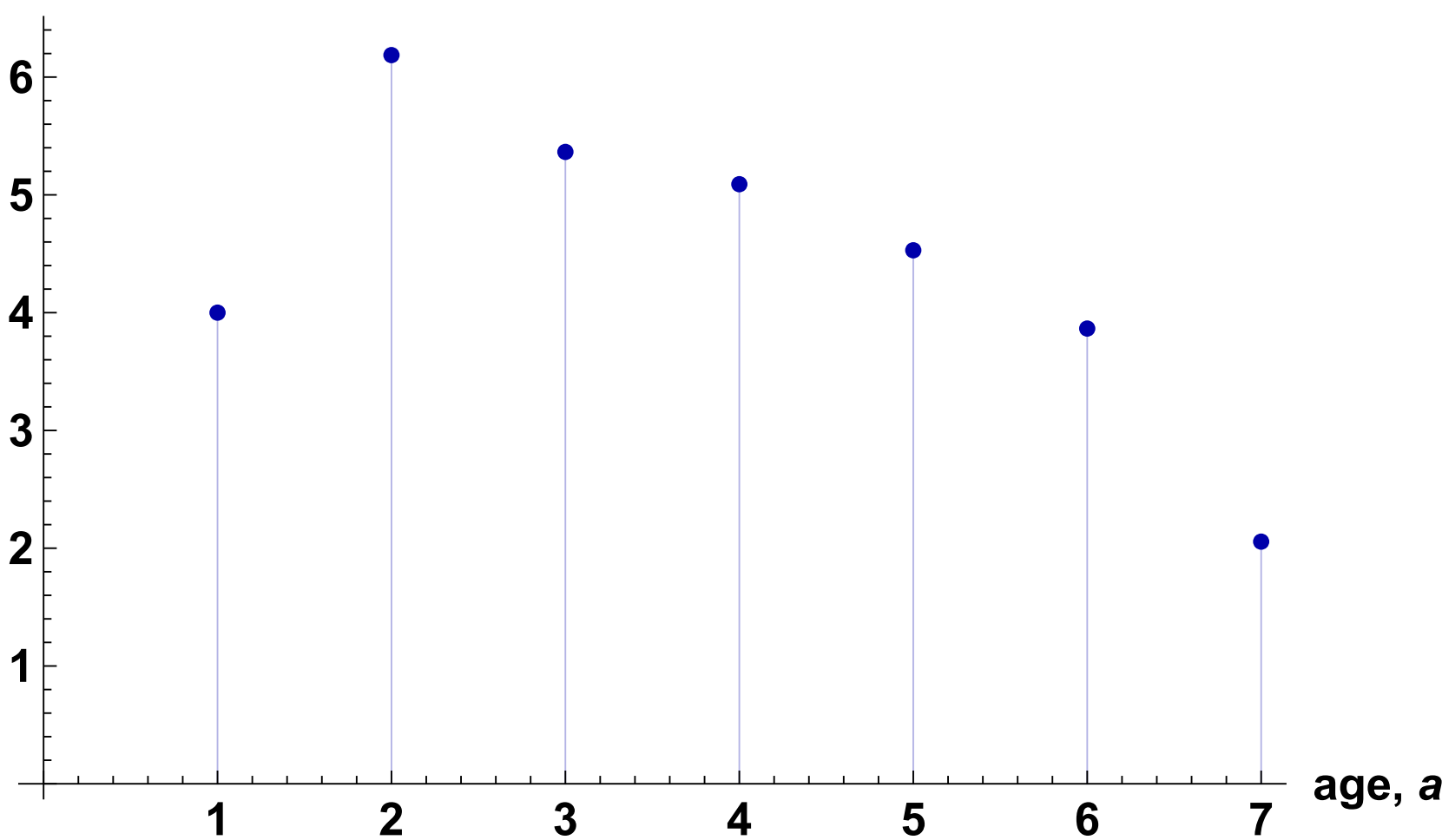
Age $a$ (years)	$p_a$	$m_a$	$f_a$
0	0.25		
1	0.46	1.15	0.32
2	0.77	2.05	0.57
3	0.65	2.05	0.57
4	0.67	2.05	0.57
5	0.64	2.05	0.57
6	0.88	2.05	0.57
7		2.05	0.57

probability of survival till  $a$ ,  $l_a$



selection on fecundity decreases with age

reproductive value,  $v_a$



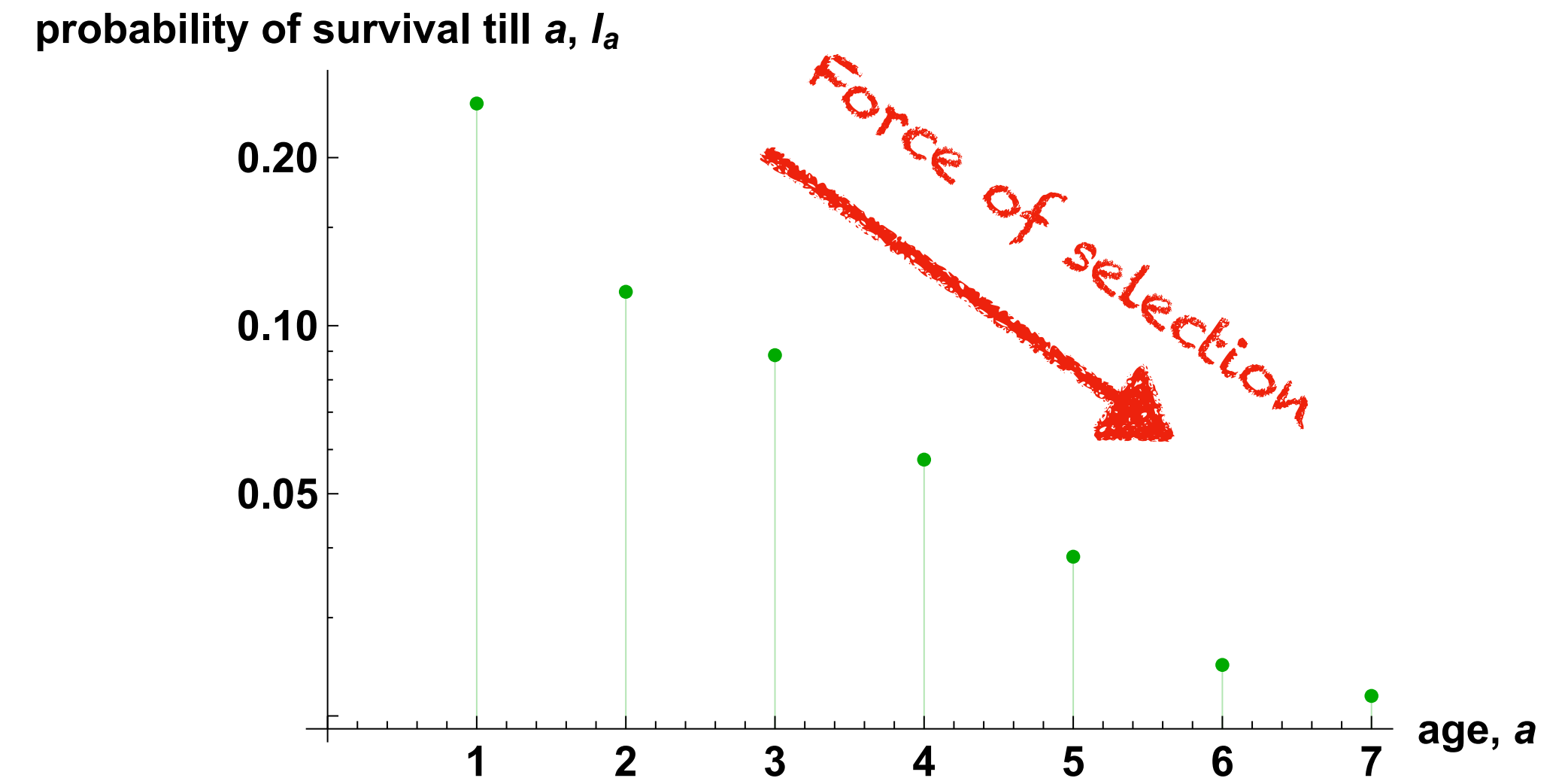
selection on survival biased towards  
ages with greatest perspective of  
reproduction



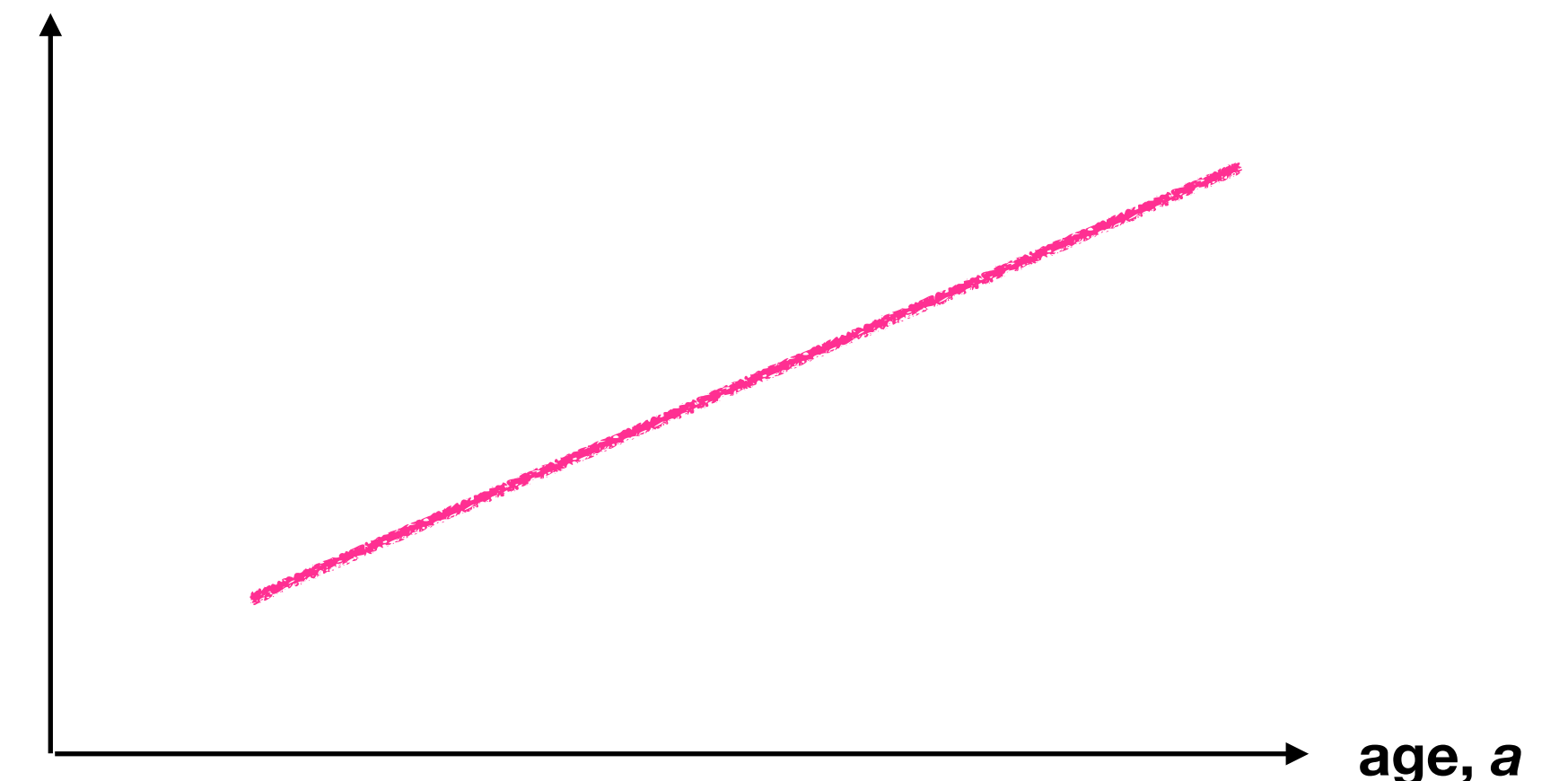
# Mutation accumulation

## 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.



Frequency of deleterious mutation acting at age  $a$



# Antagonistic pleiotropy

**Williams 1957**

- Where one trait or gene improves early vital rates but worsen later ones.

# Antagonistic pleiotropy

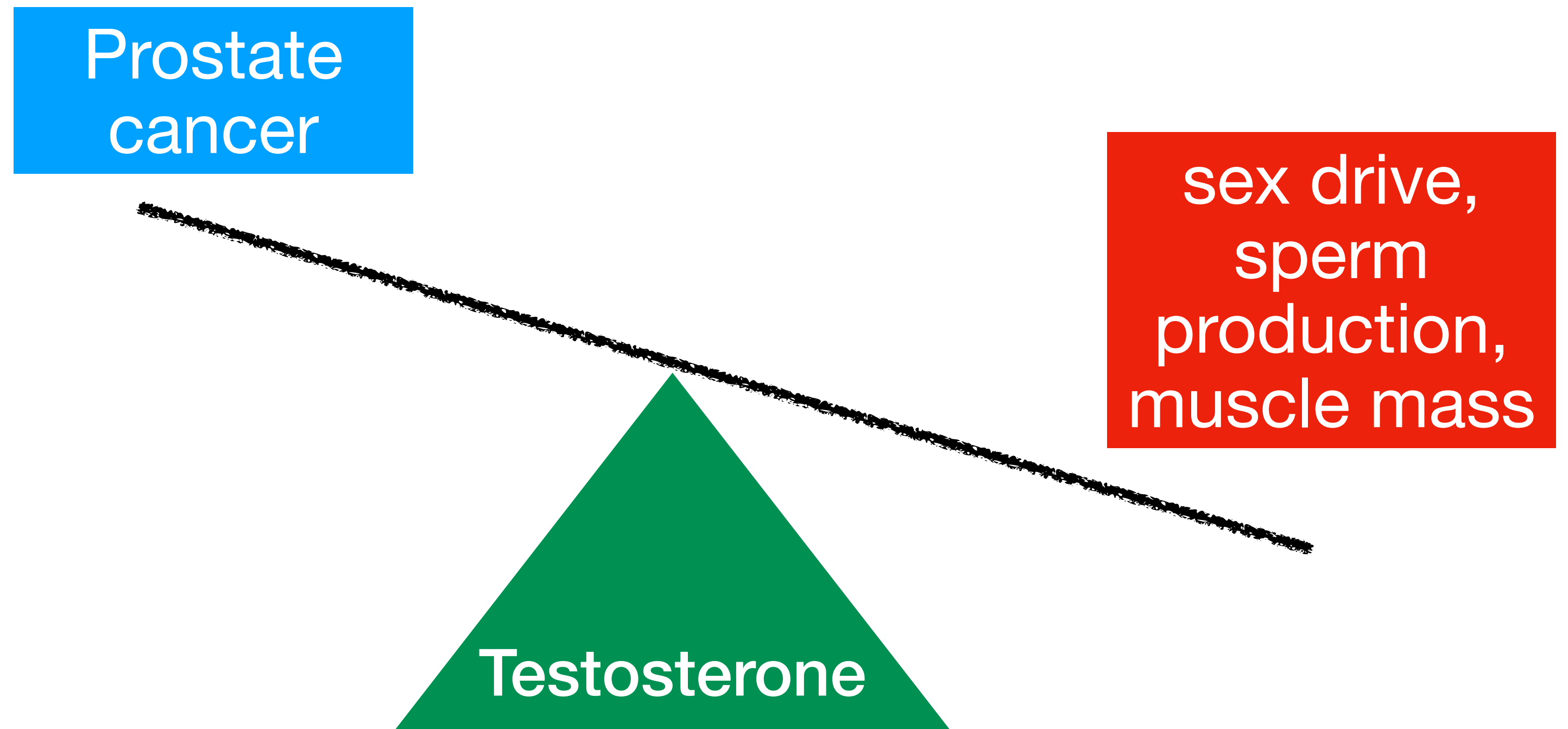
**Williams 1957**

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- As selection is stronger on early effects, evolution will favour such a trait at the expense of later life.

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# Disposable soma theory

Kirkwood 1977

- A mechanism for trade-off and antagonistic pleiotropy.

# Disposable soma theory

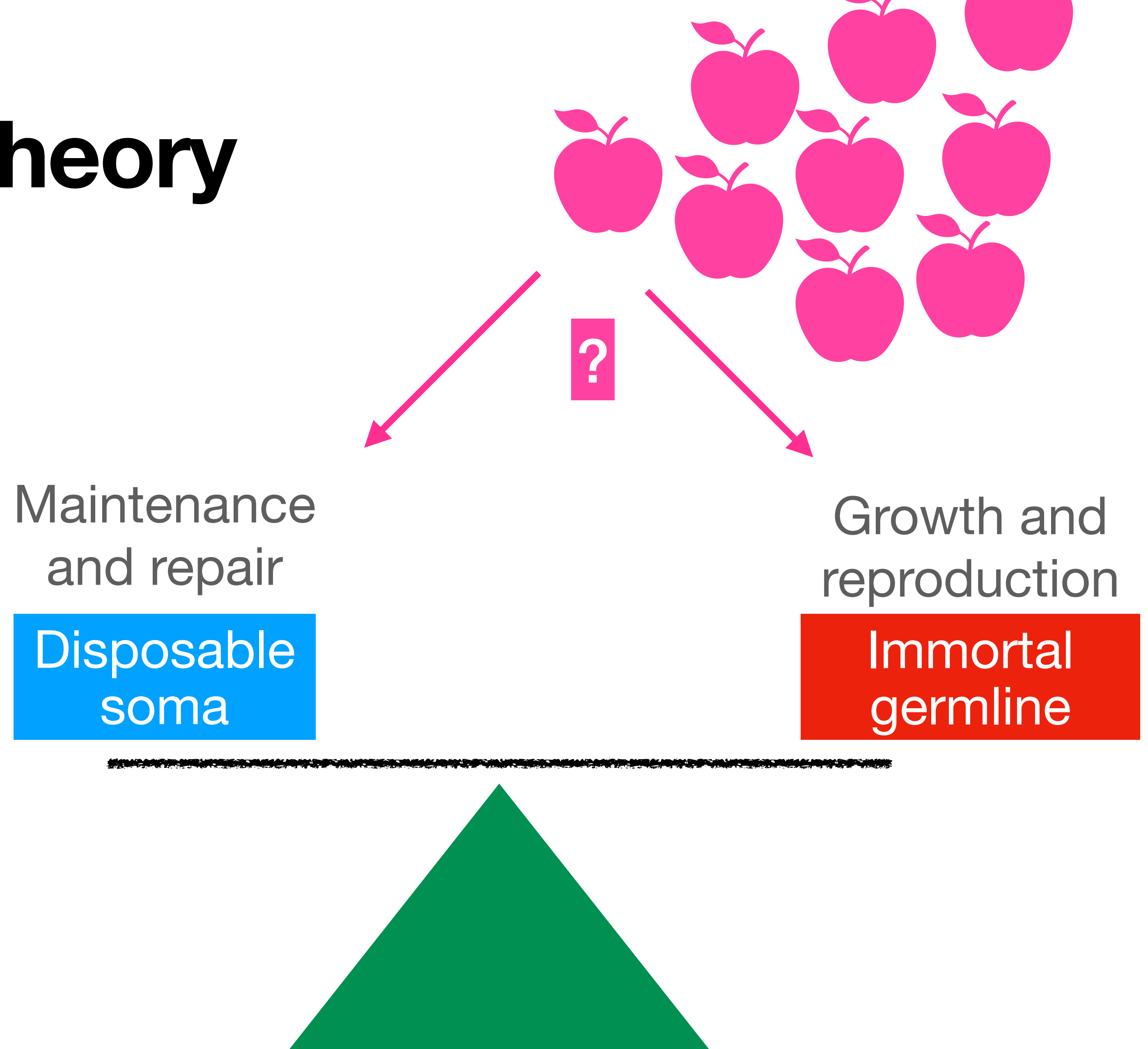
Kirkwood 1977

- A mechanism for trade-off and antagonistic pleiotropy.
- Because resources are limited, organisms need to decide whether to invest their finite energy into mechanisms that boost fecundity (i.e., the germline) or non-reproductive mechanisms (i.e., the soma) that combat ageing.

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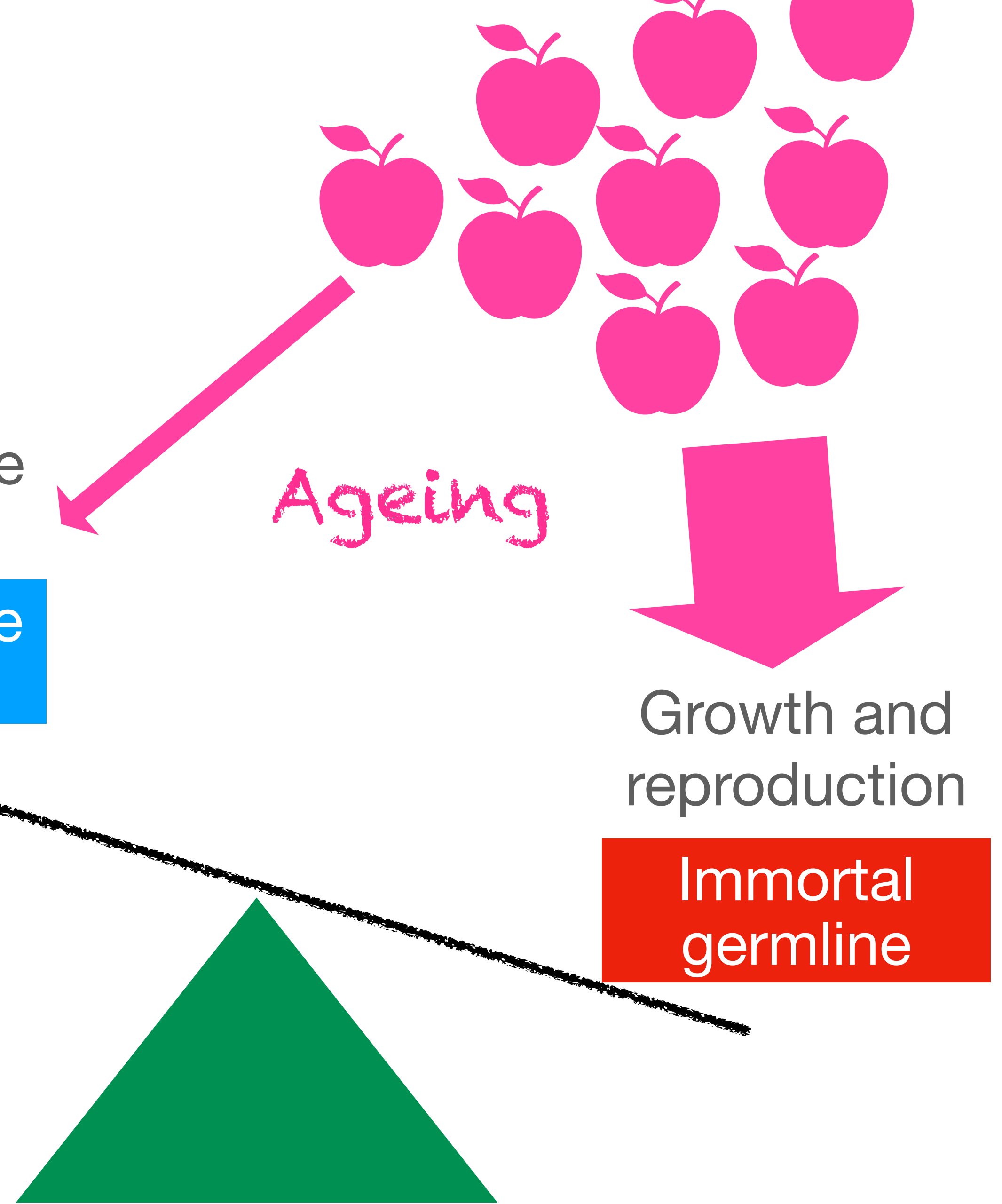
Maintenance  
and repair

Disposable  
soma

Ageing

Growth and  
reproduction

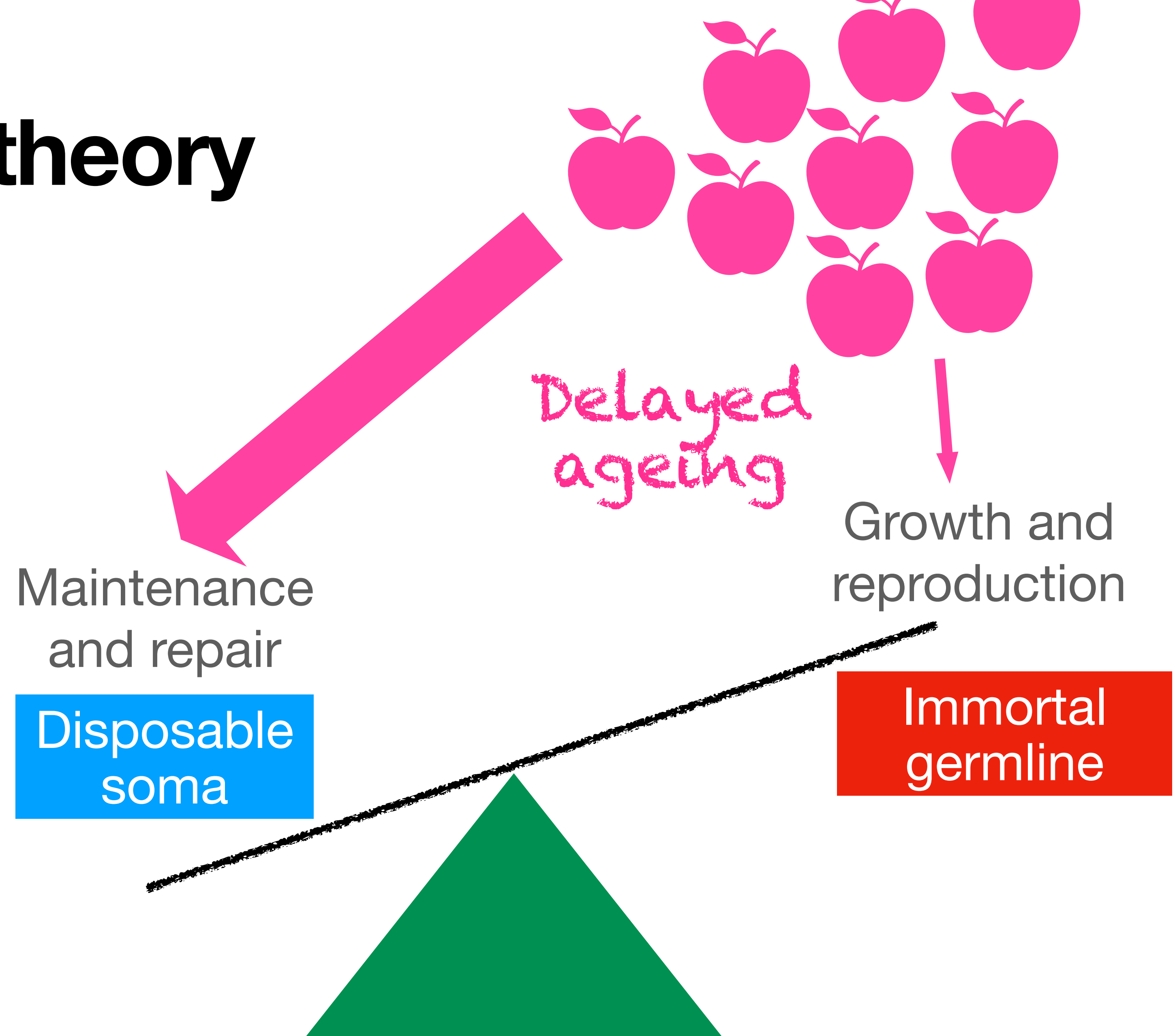
Immortal  
germline



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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)

