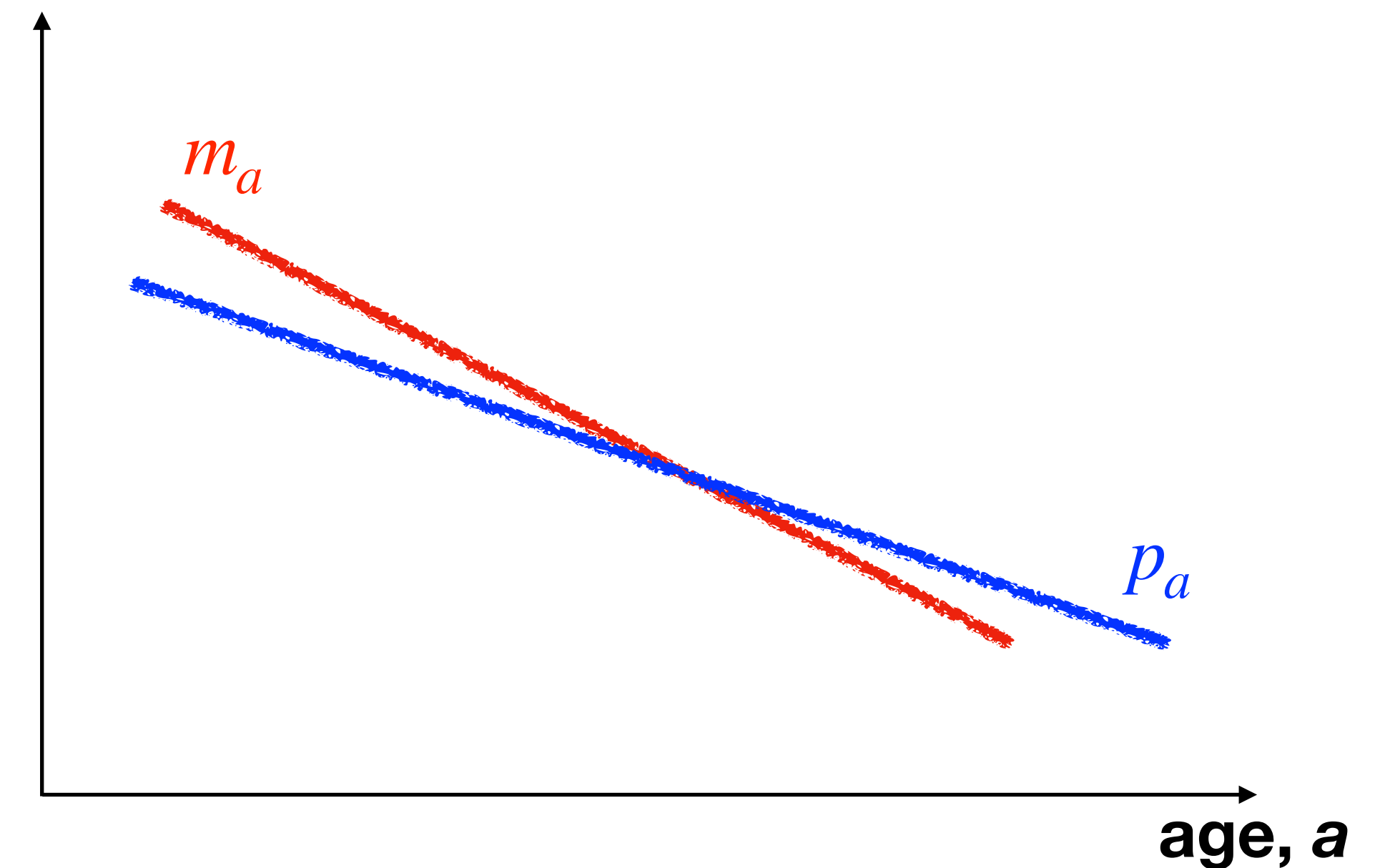
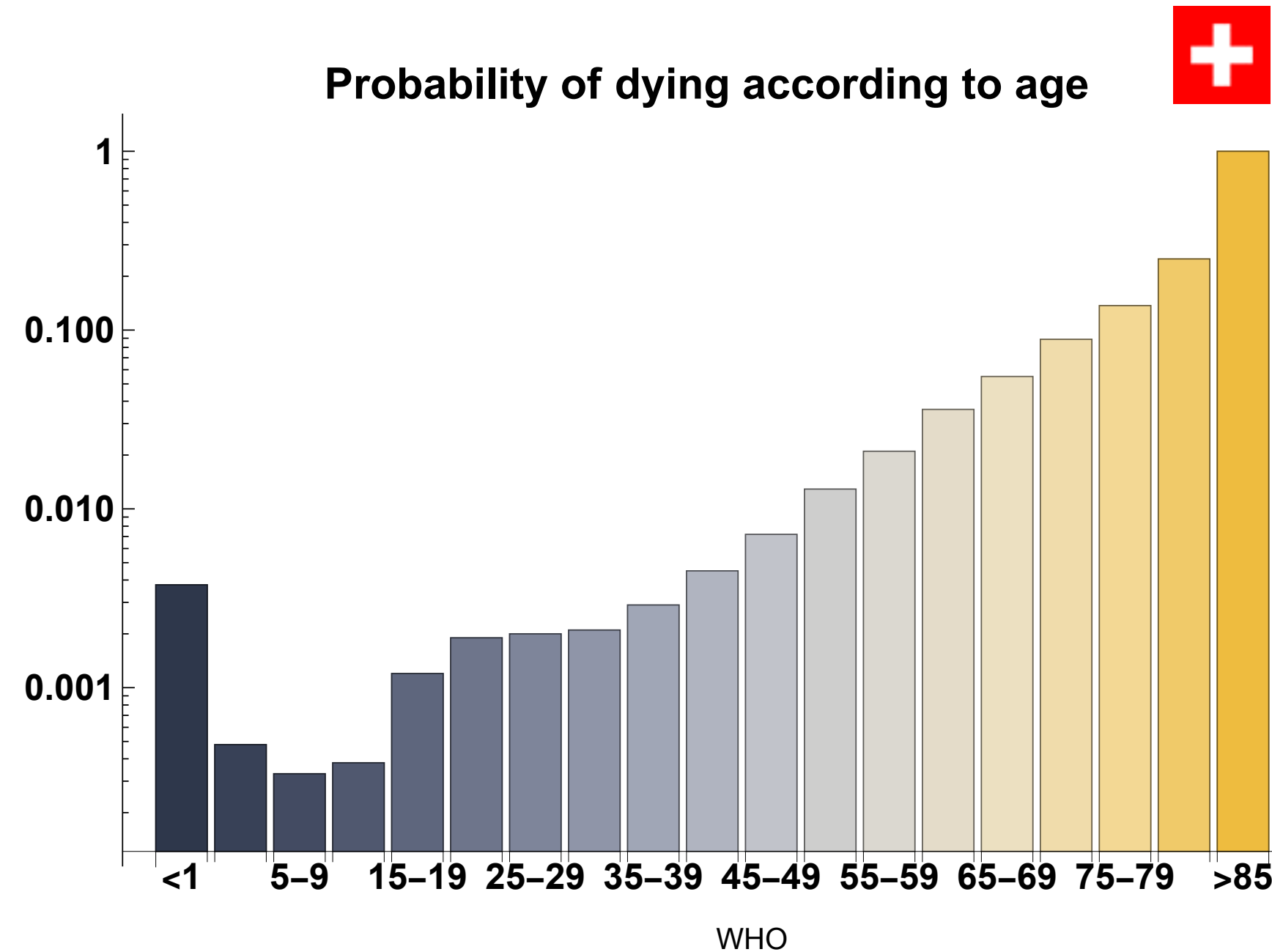


Evolution of ageing

Recap on ageing

- 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 , i.e.
expected number of offspring given
survival till age a

$$= v_{a+1}(x) = \sum_{b=a+1}^{\infty} \frac{l_b(x)}{l_{a+1}(x)} m_b(x)$$

Strength of selection decreases with age

Hamilton 1966

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

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selection is
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survival till relevant
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Strength of selection decreases with age

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Survival
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 a

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

selection is
proportional to
survival till relevant
age

selection on
survival
proportional to
reproductive value

Strength of selection decreases with age

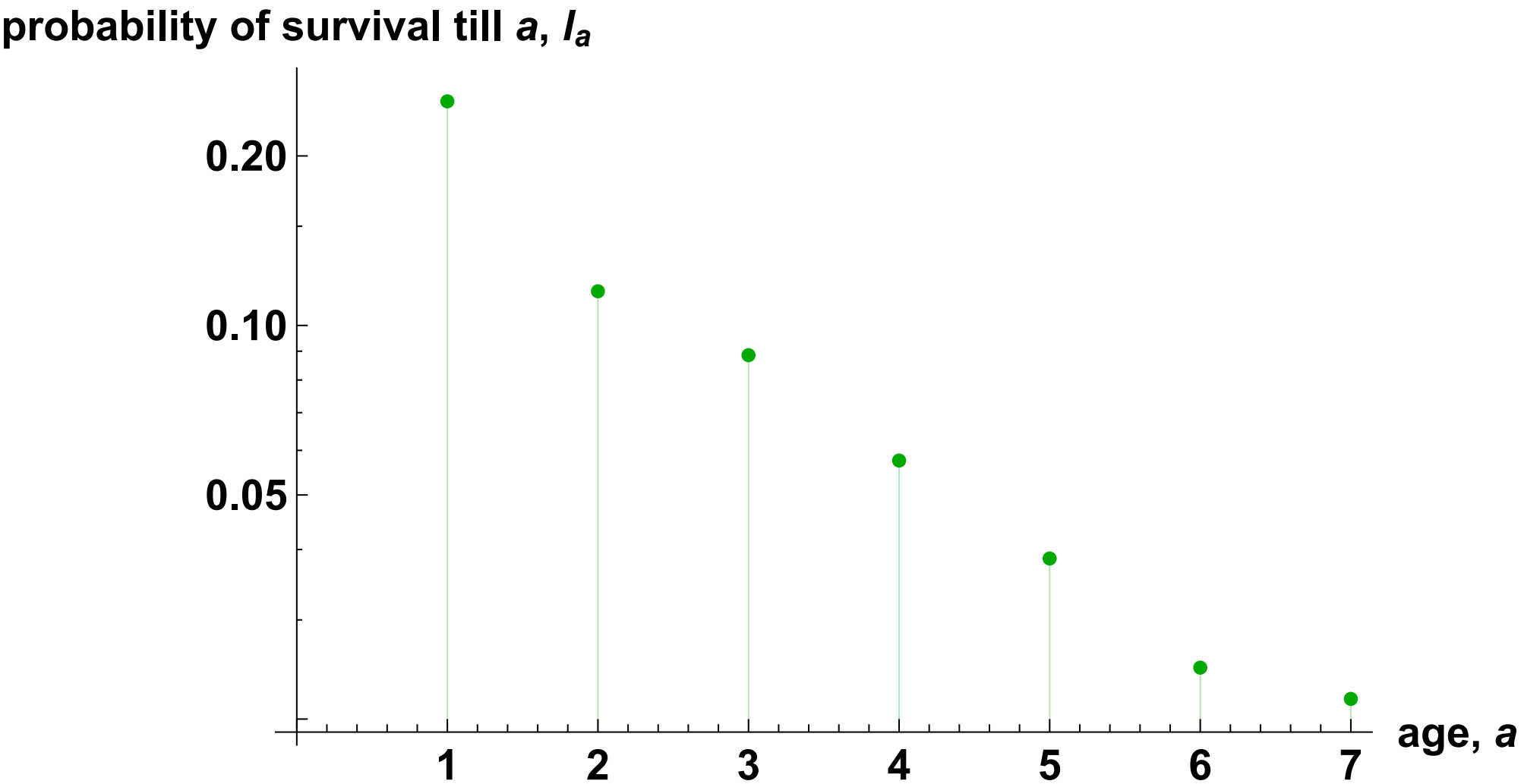
Gray squirrel example (with fecundity scaled so that $R_0 = 1$)

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

Strength of selection decreases with age

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

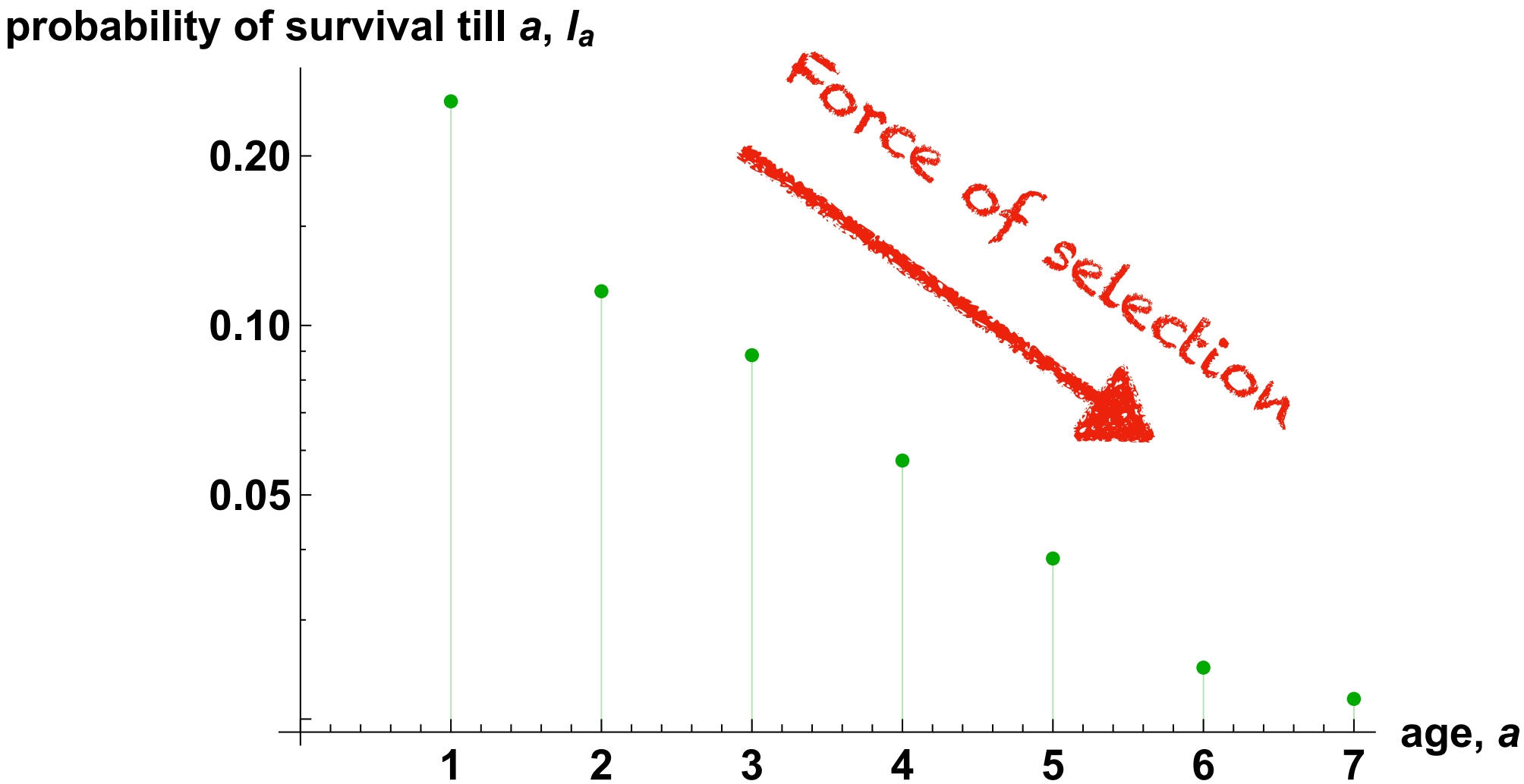
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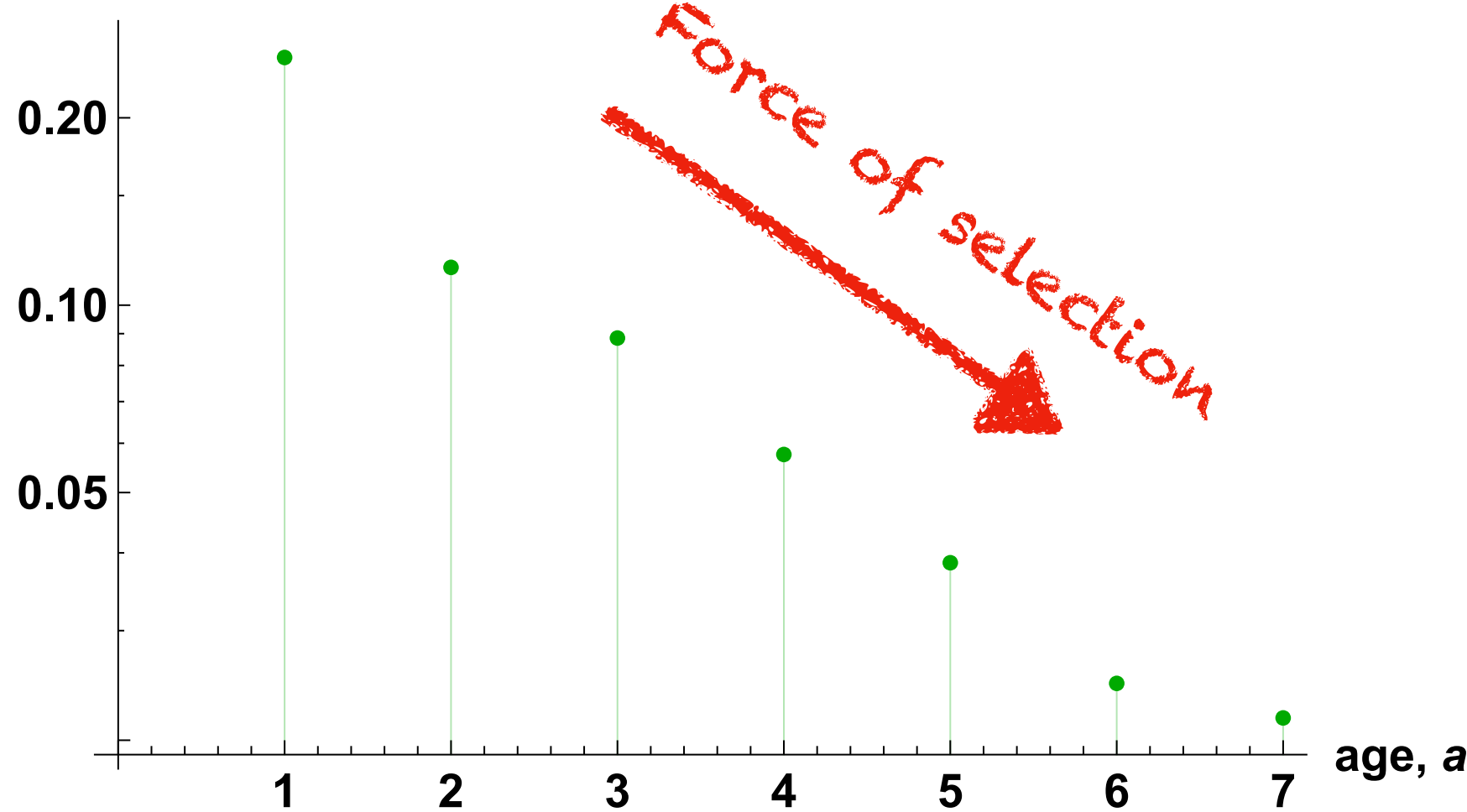
selection on fecundity decreases with age

Strength of selection decreases with age

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

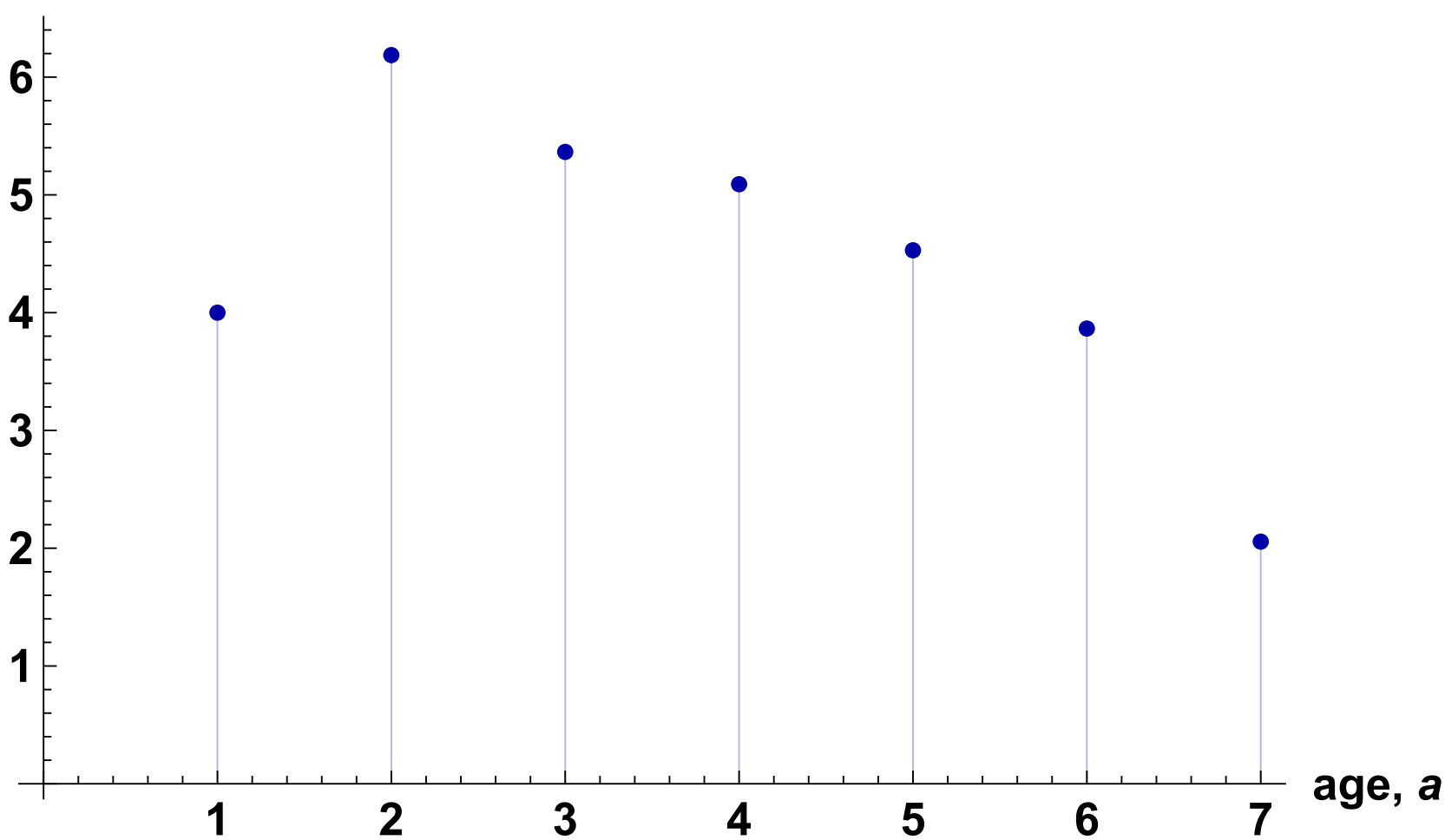
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probability of survival till a , l_a



selection on fecundity decreases with age

reproductive value, v_a

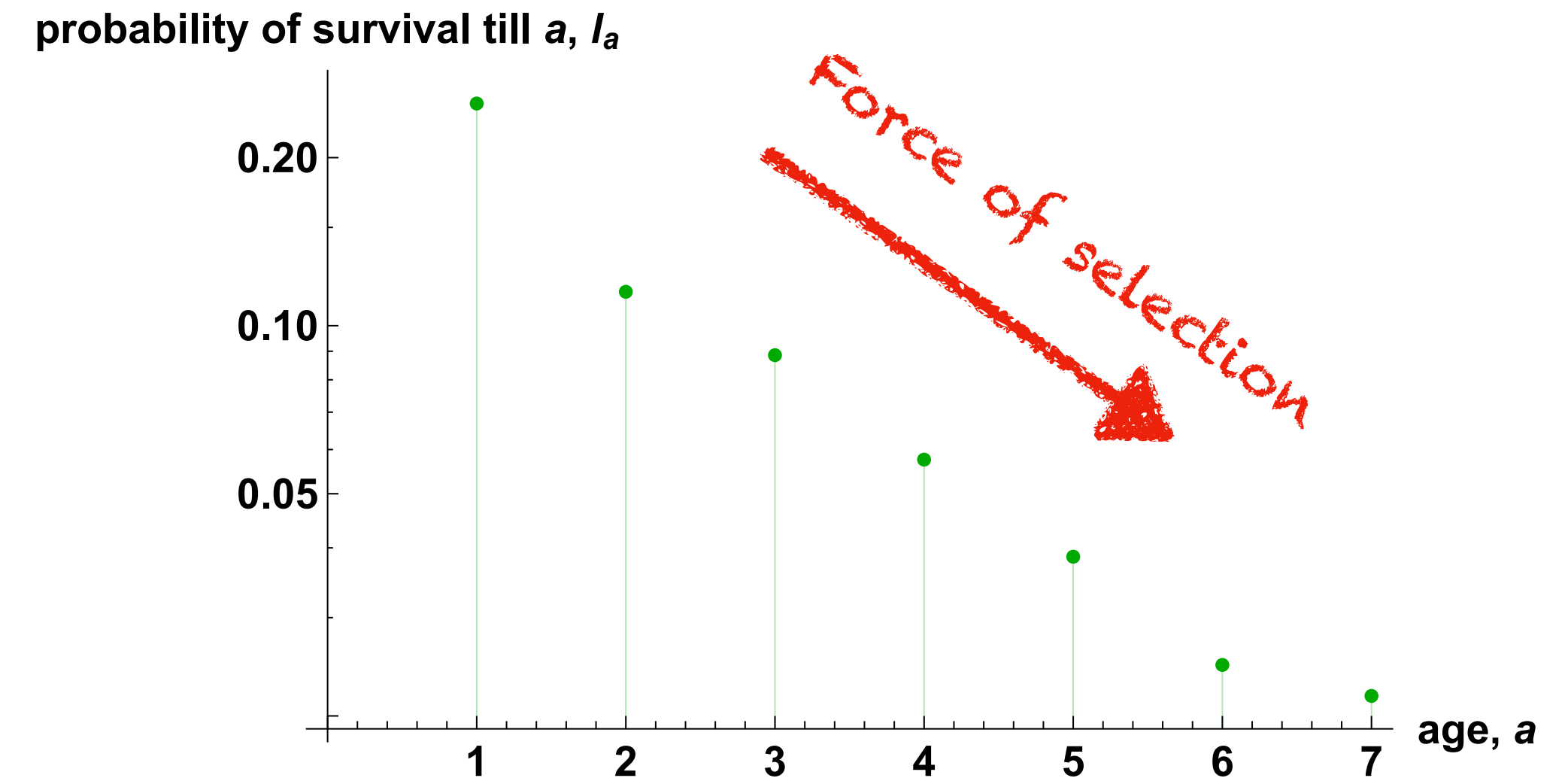


selection on survival biased towards
ages with greatest perspective of
reproduction

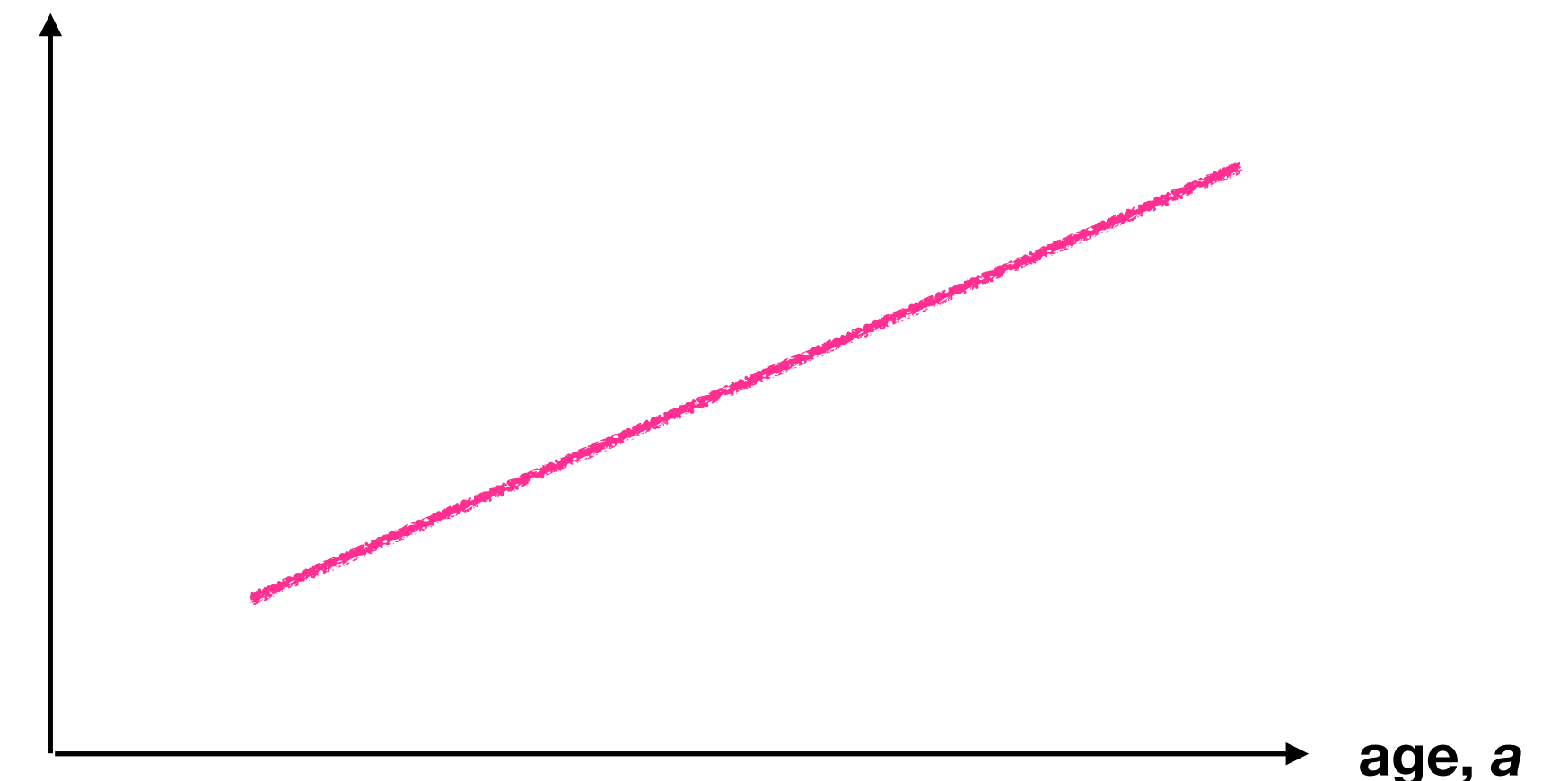
Mutation accumulation

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

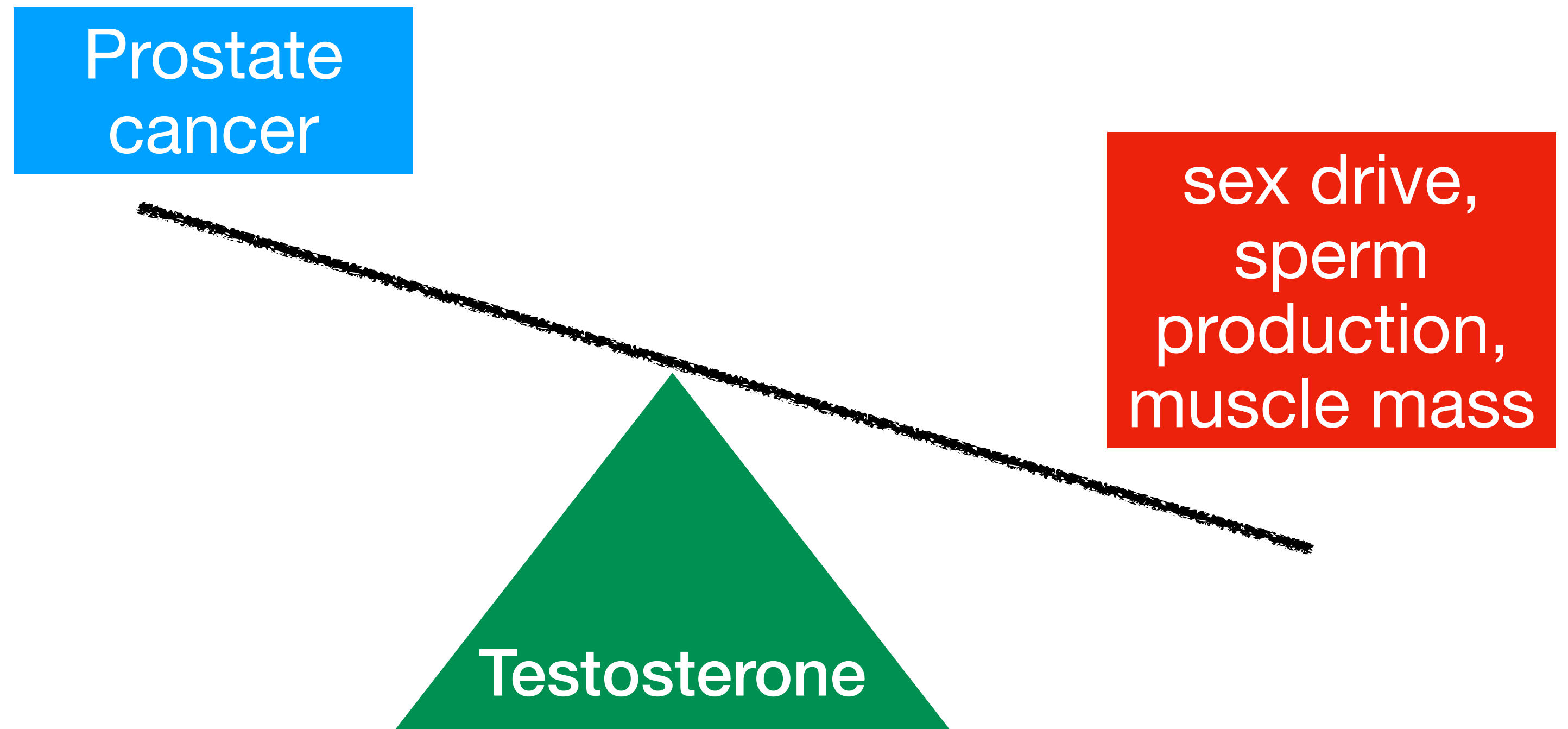
Williams 1957

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Disposable soma theory

Kirkwood 1977

- A mechanism for trade-off and antagonistic pleiotropy.

Disposable soma theory

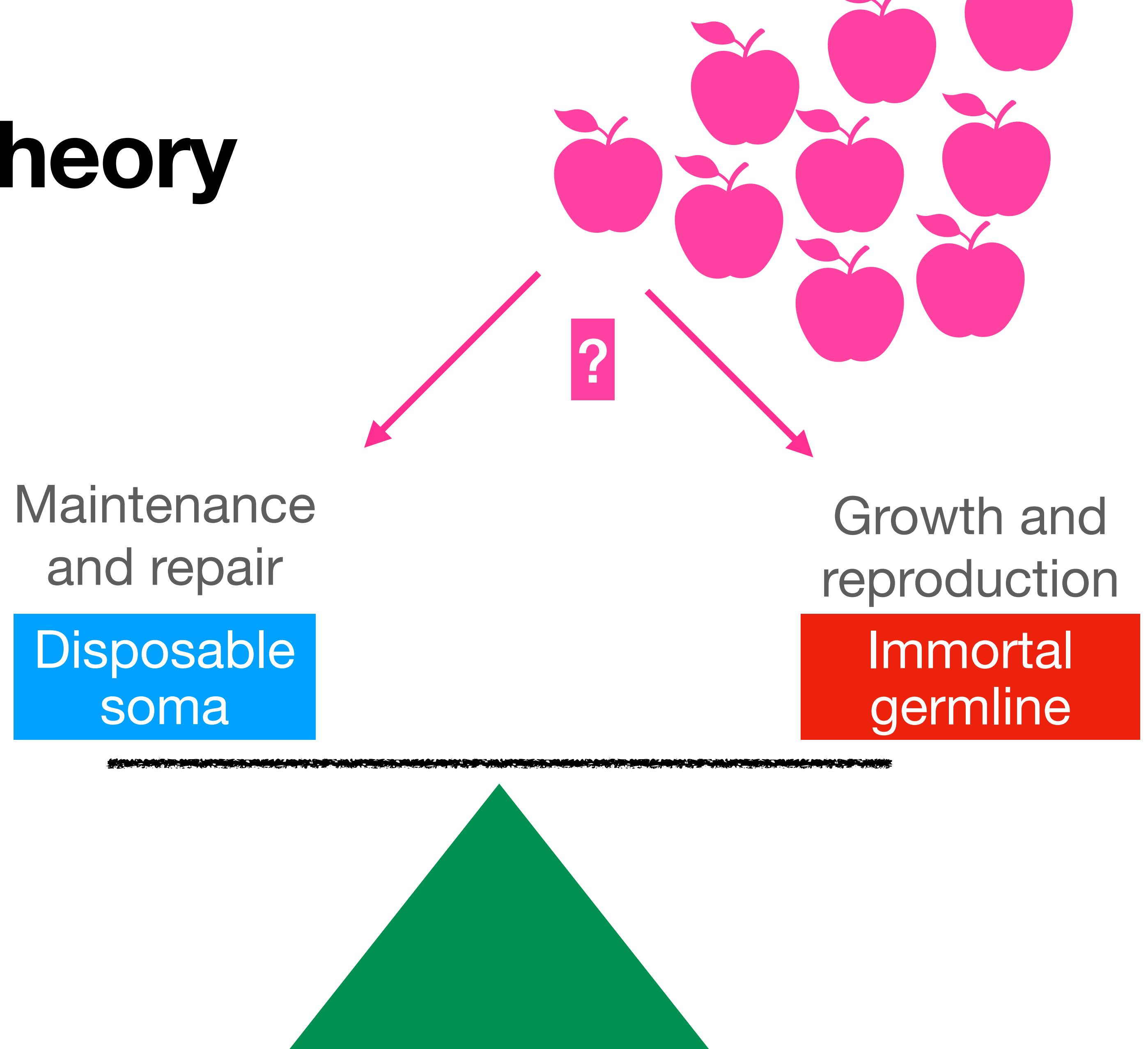
Kirkwood 1977

- 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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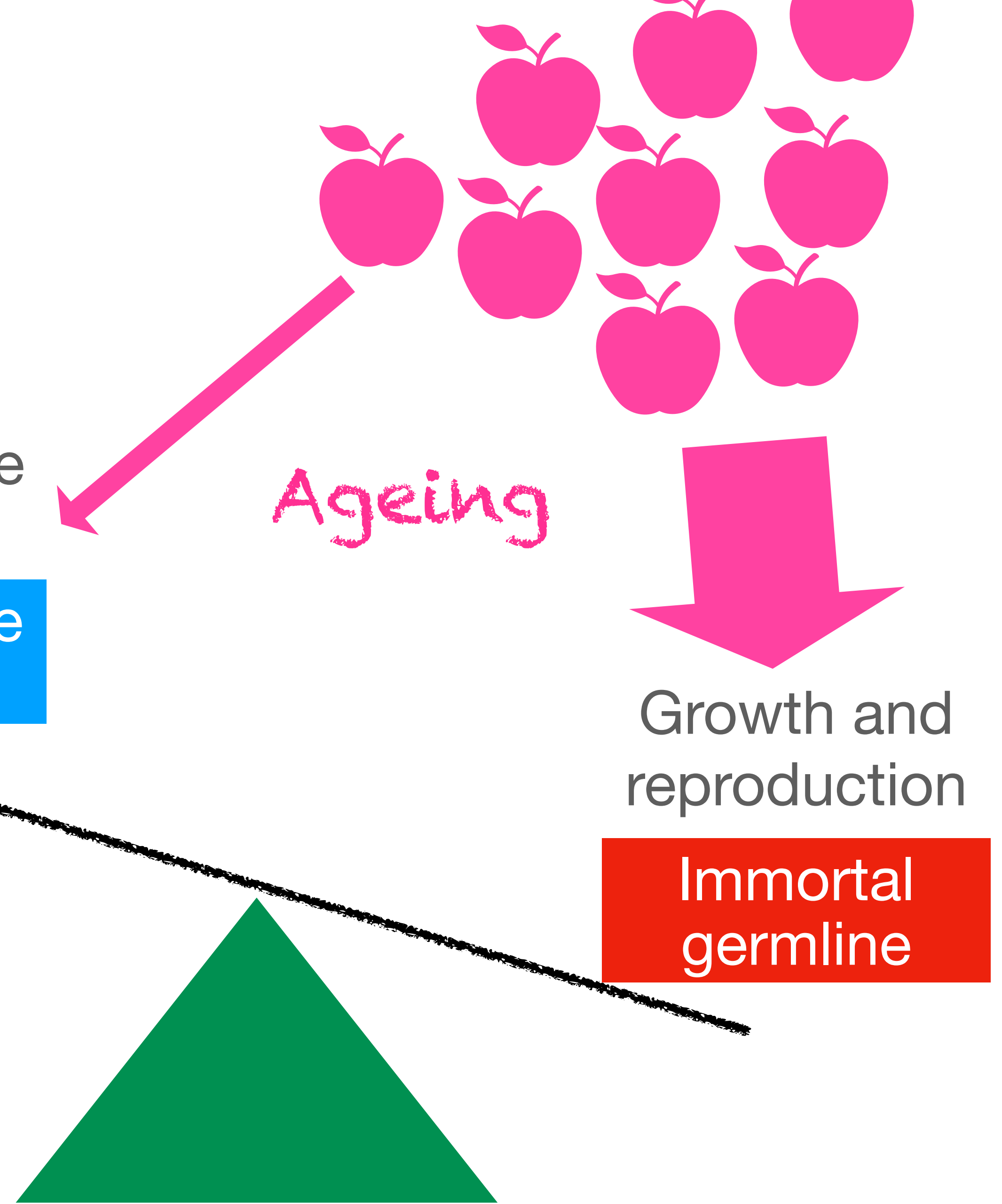
Maintenance
and repair

Disposable
soma

Ageing

Growth and
reproduction

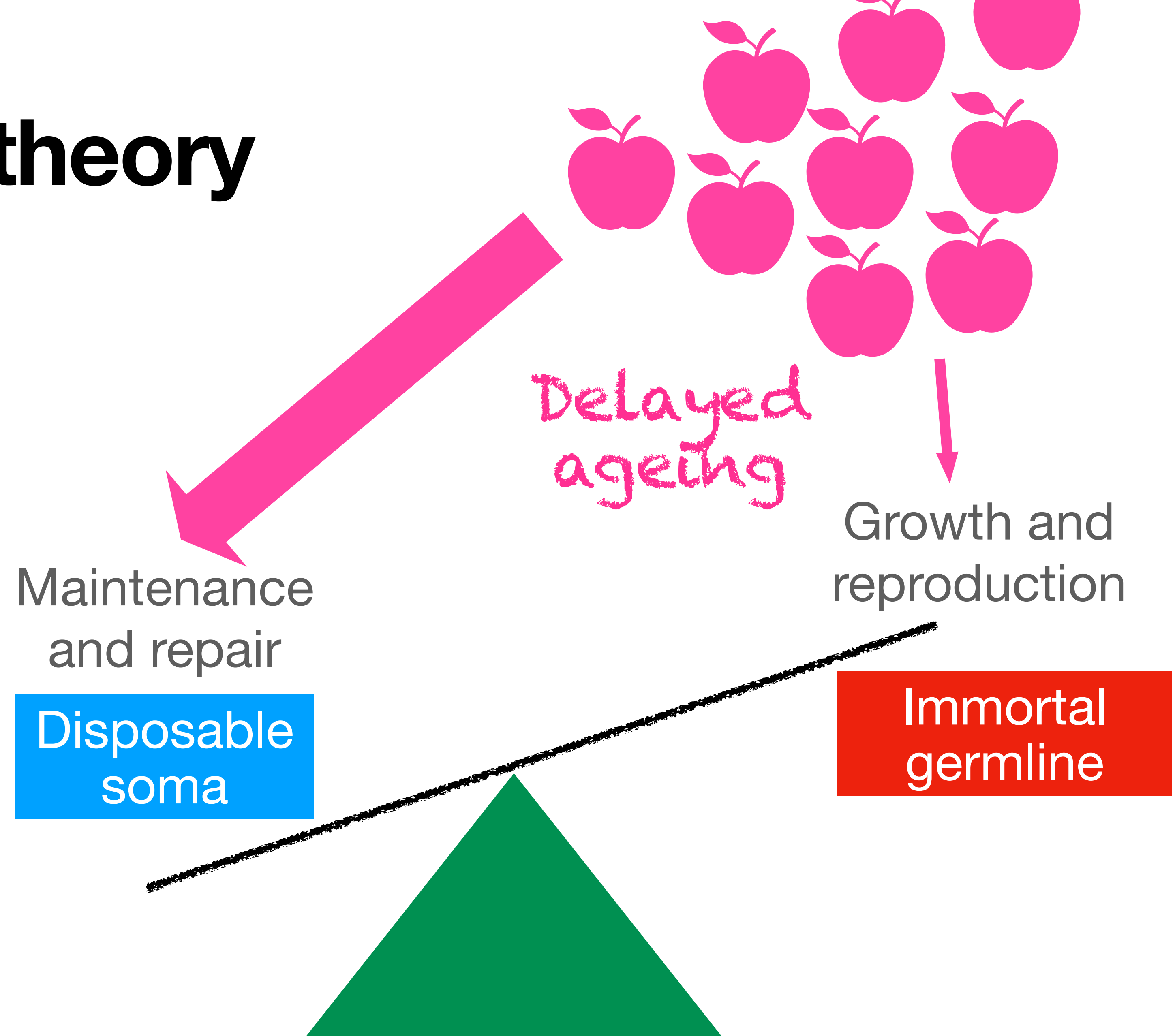
Immortal
germline



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Summary

- 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)

