

# **Part III - Foraging theory**

**Sex, Ageing and Foraging Theory**

**resources**

**energy**

**offspring**

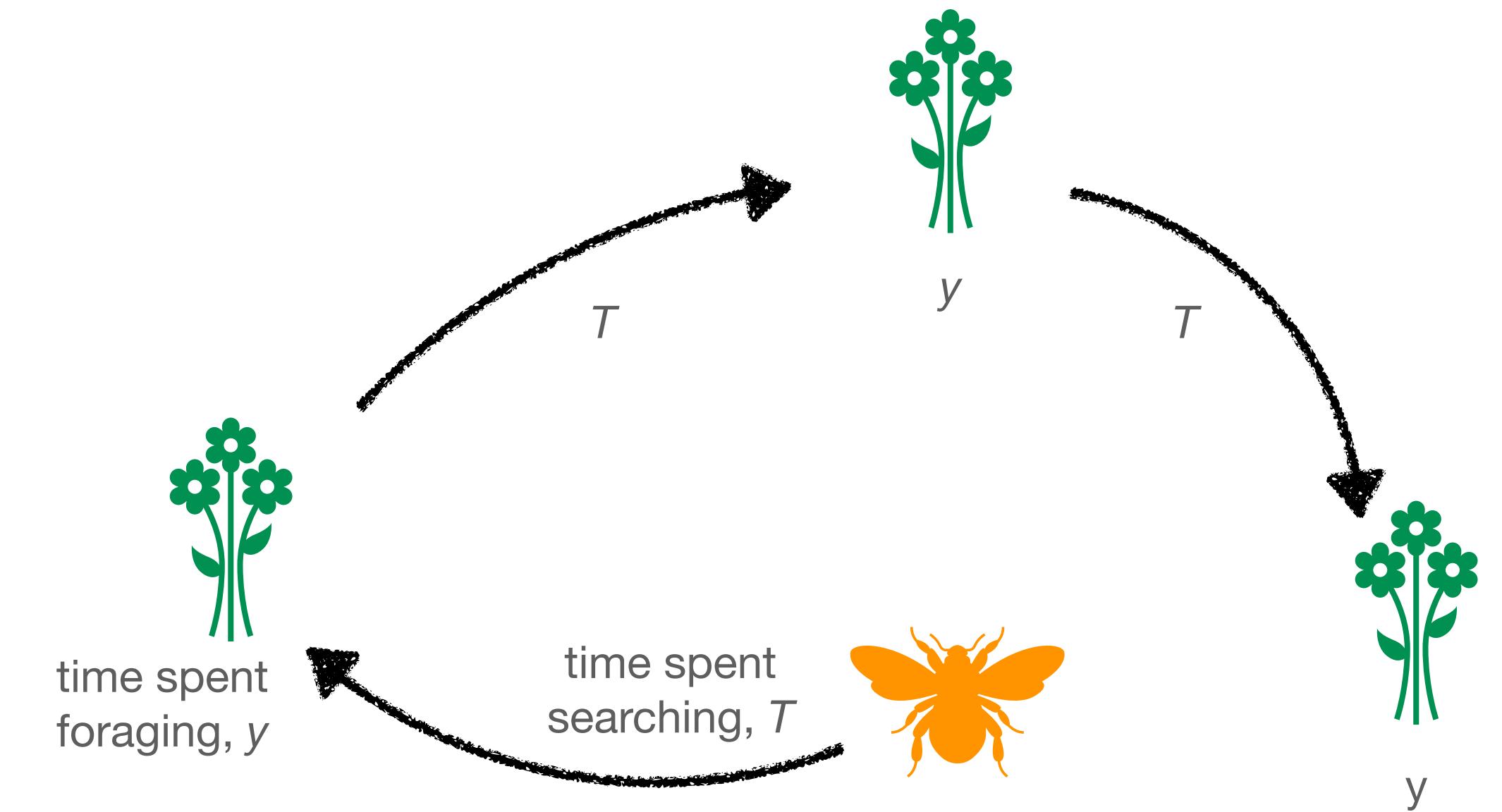
**fitness**



# Foraging in patches

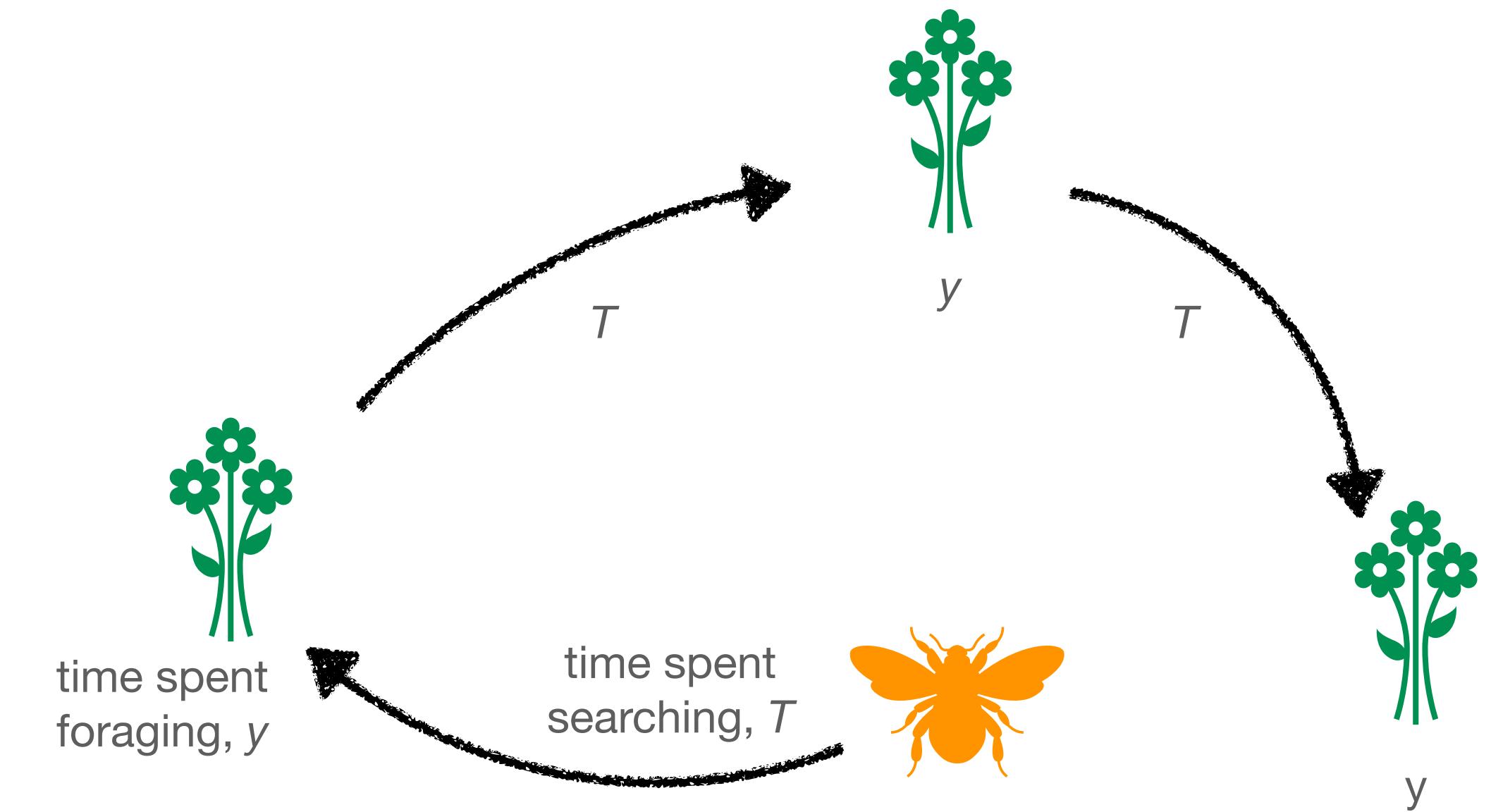
# Foraging in patches

- Animal forages on multiple equivalent patches with finite amount of resources.



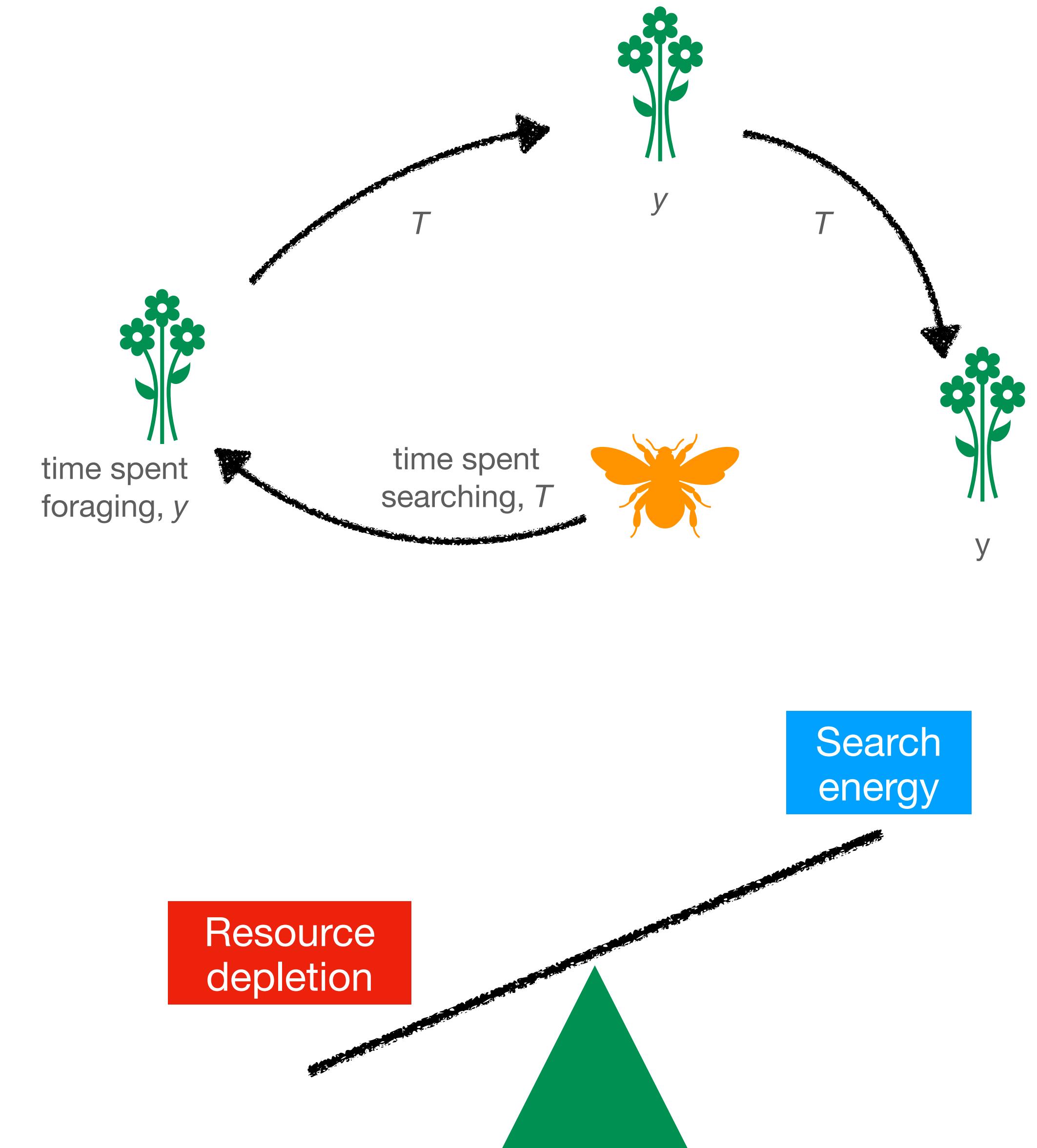
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- How much time  $y$  should it spent foraging on a single patch when searching is costly?



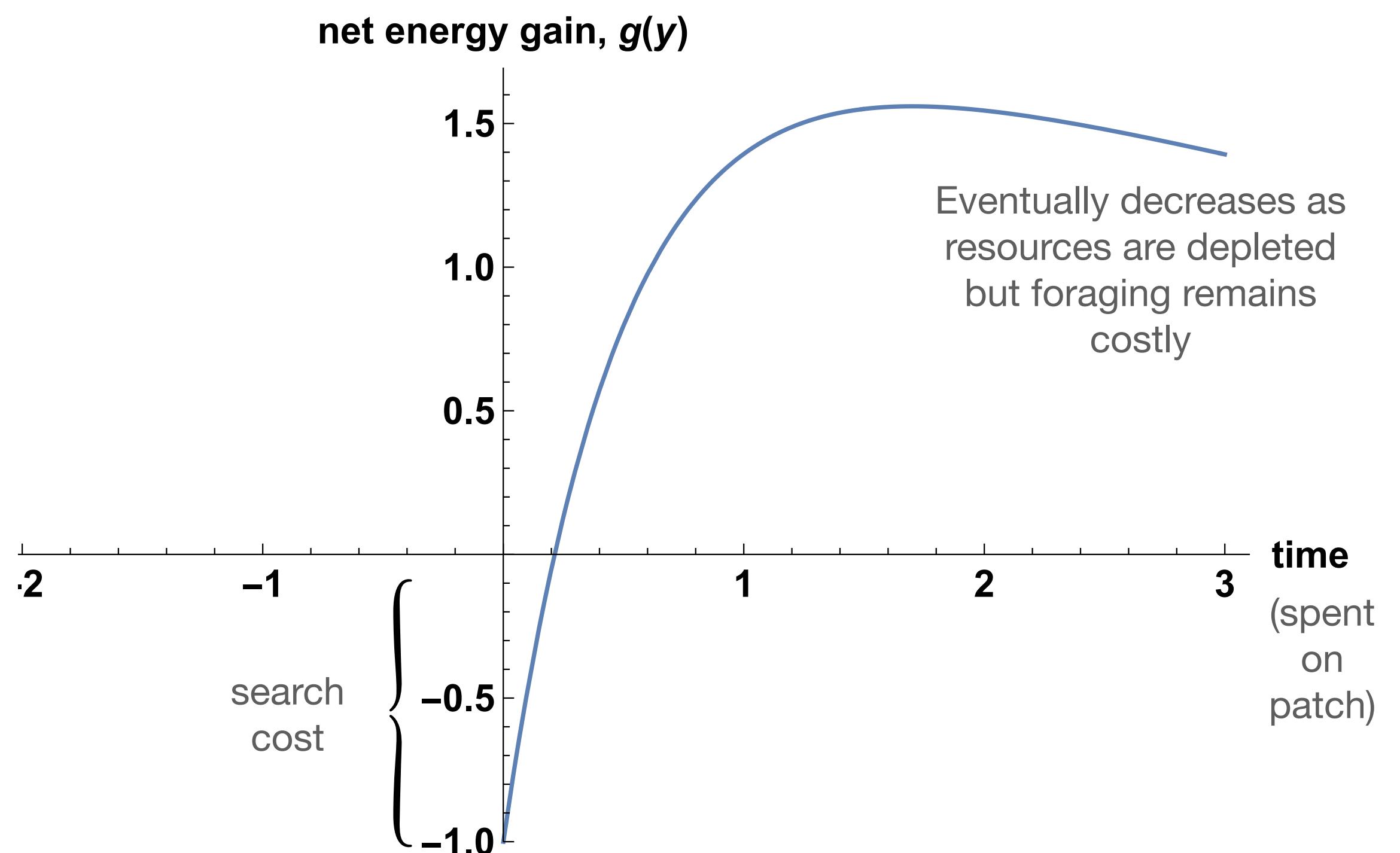
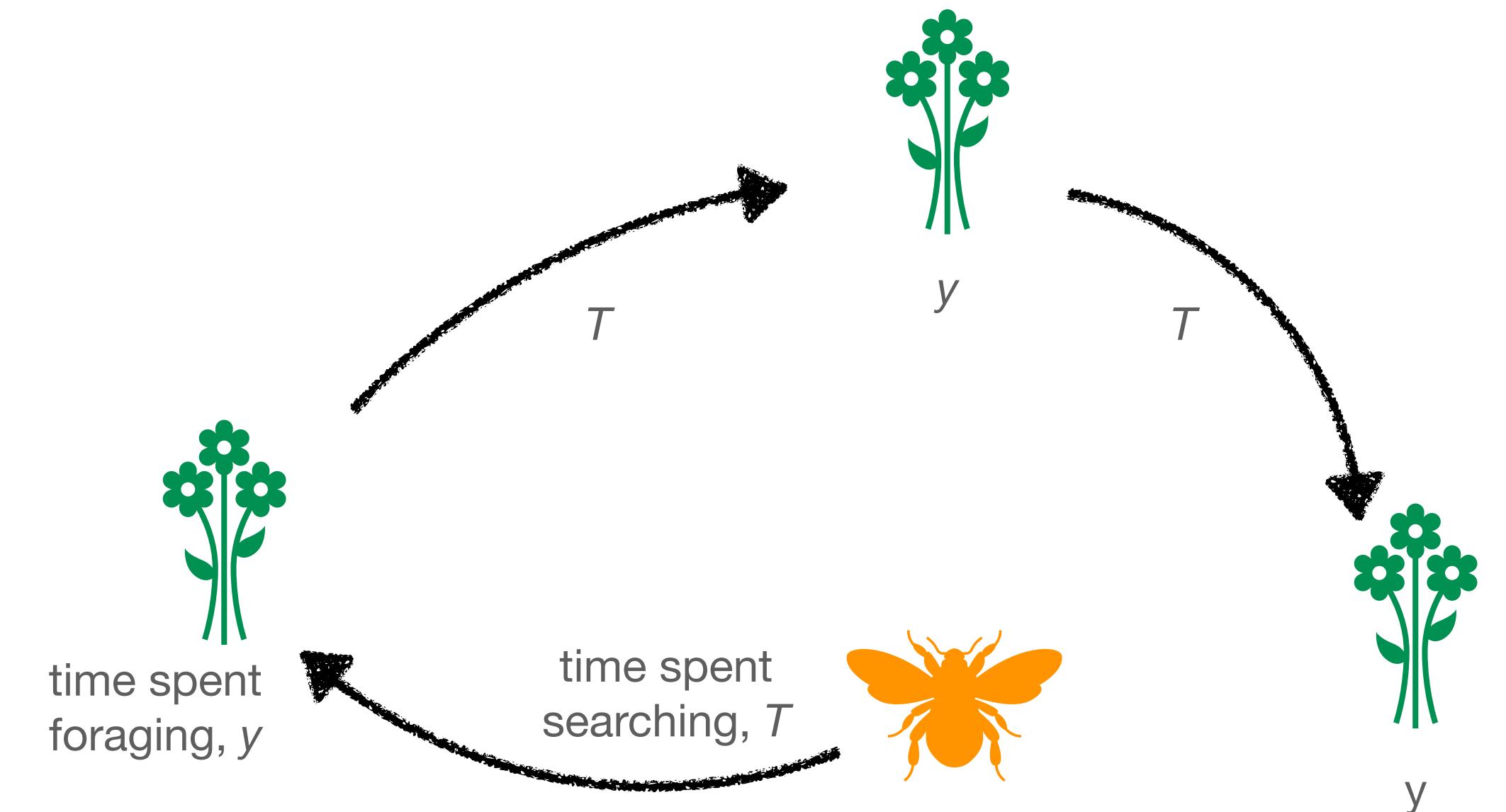
# Foraging in patches

- Animal forages on multiple equivalent patches with finite amount of resources.
- How much time  $y$  should it spent foraging on a single patch when searching is costly?
- If it stays too long, resources get depleted; too short and it does not regain energy lost from search.



# Energy gains

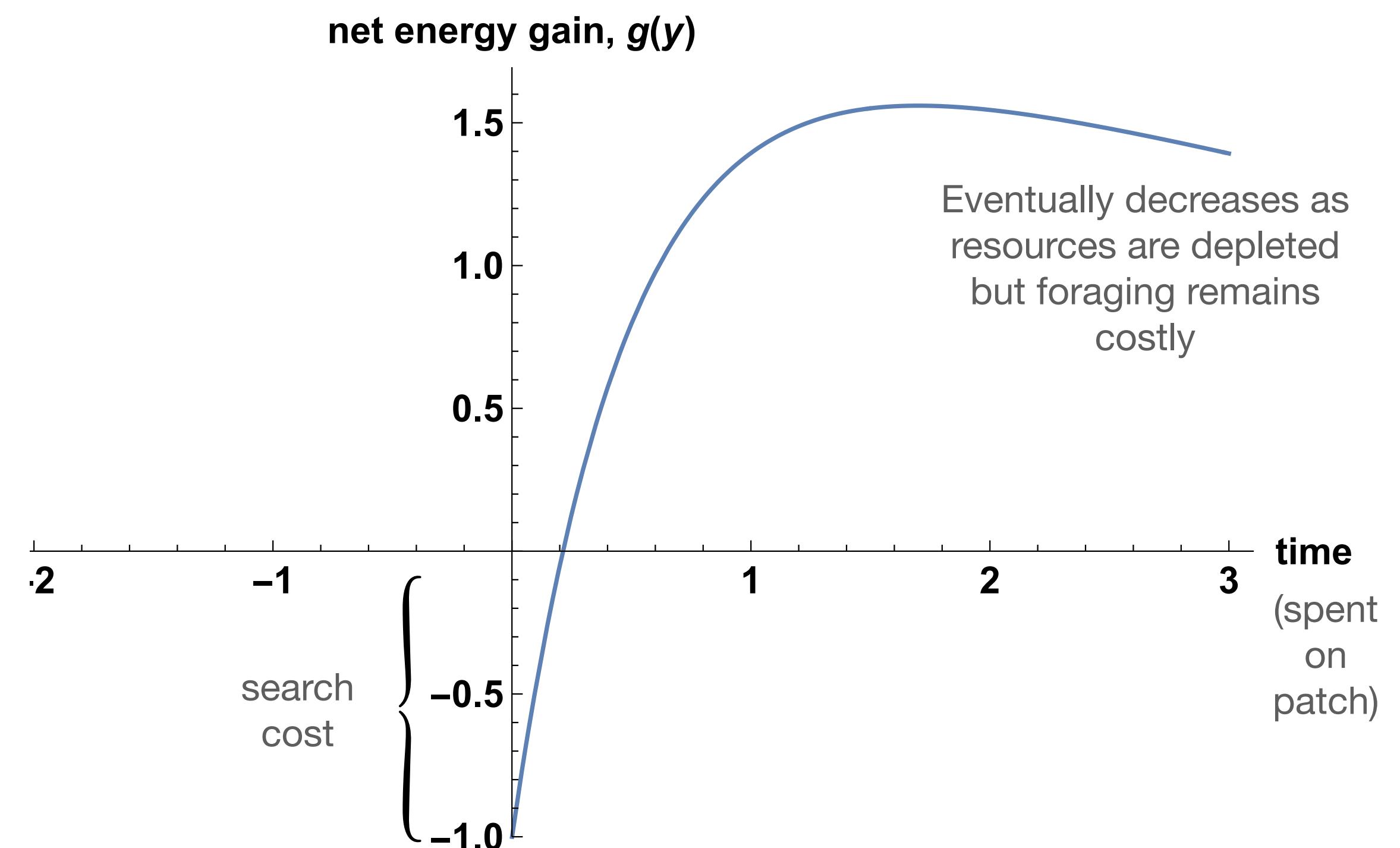
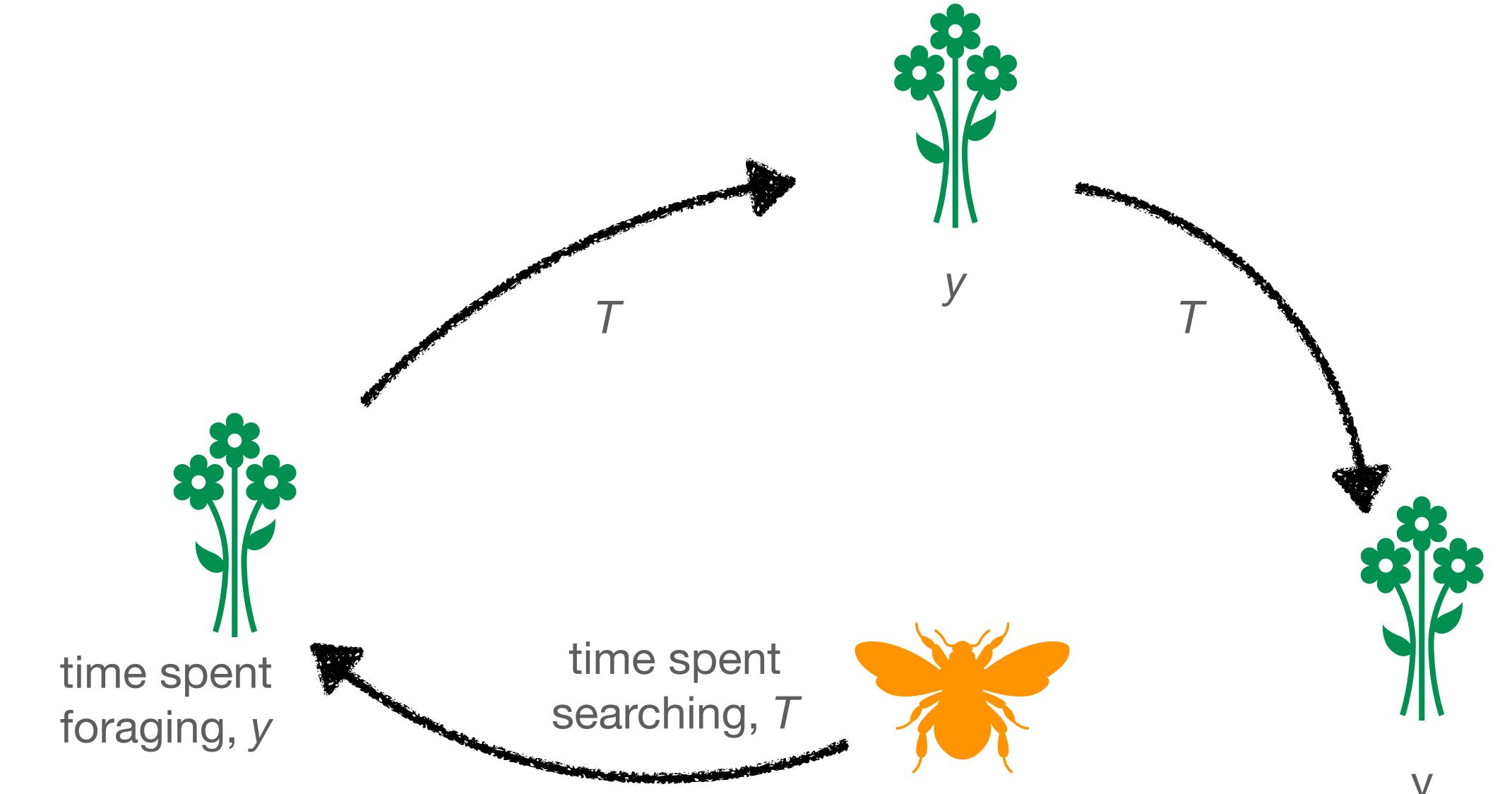
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- Rate of energy gain from search + foraging :

$$R(y) = \frac{g(y)}{y + T}$$

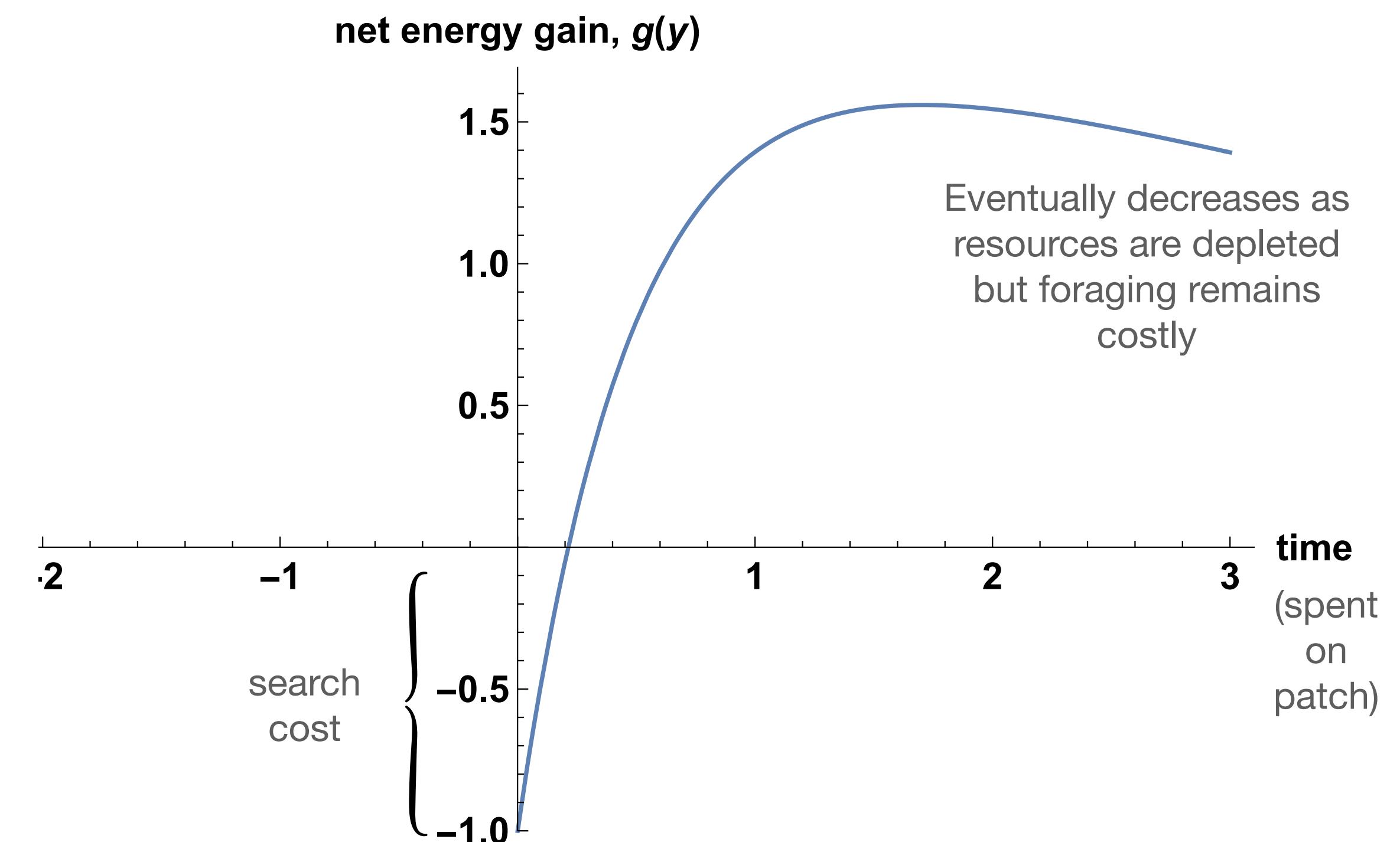
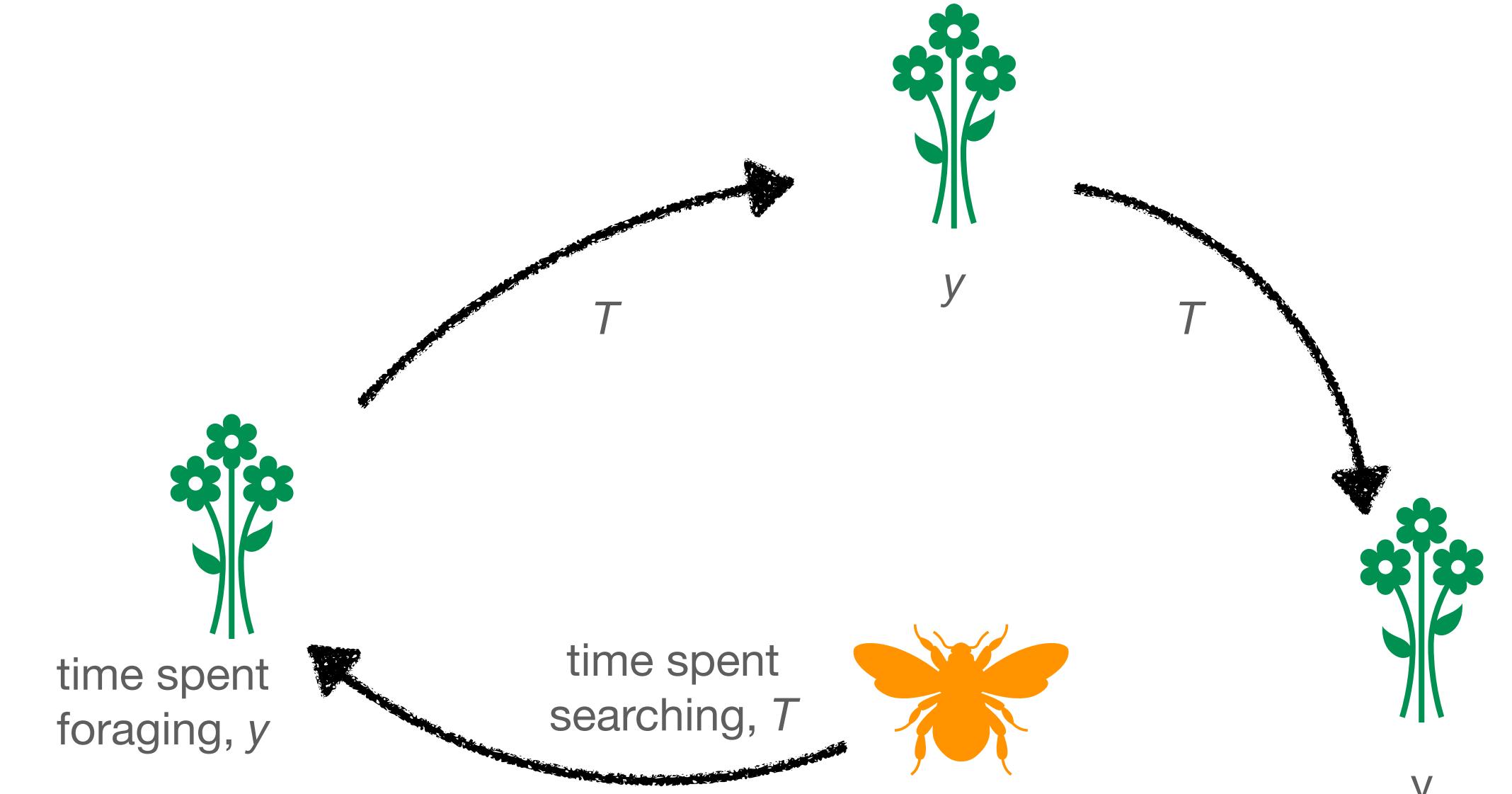


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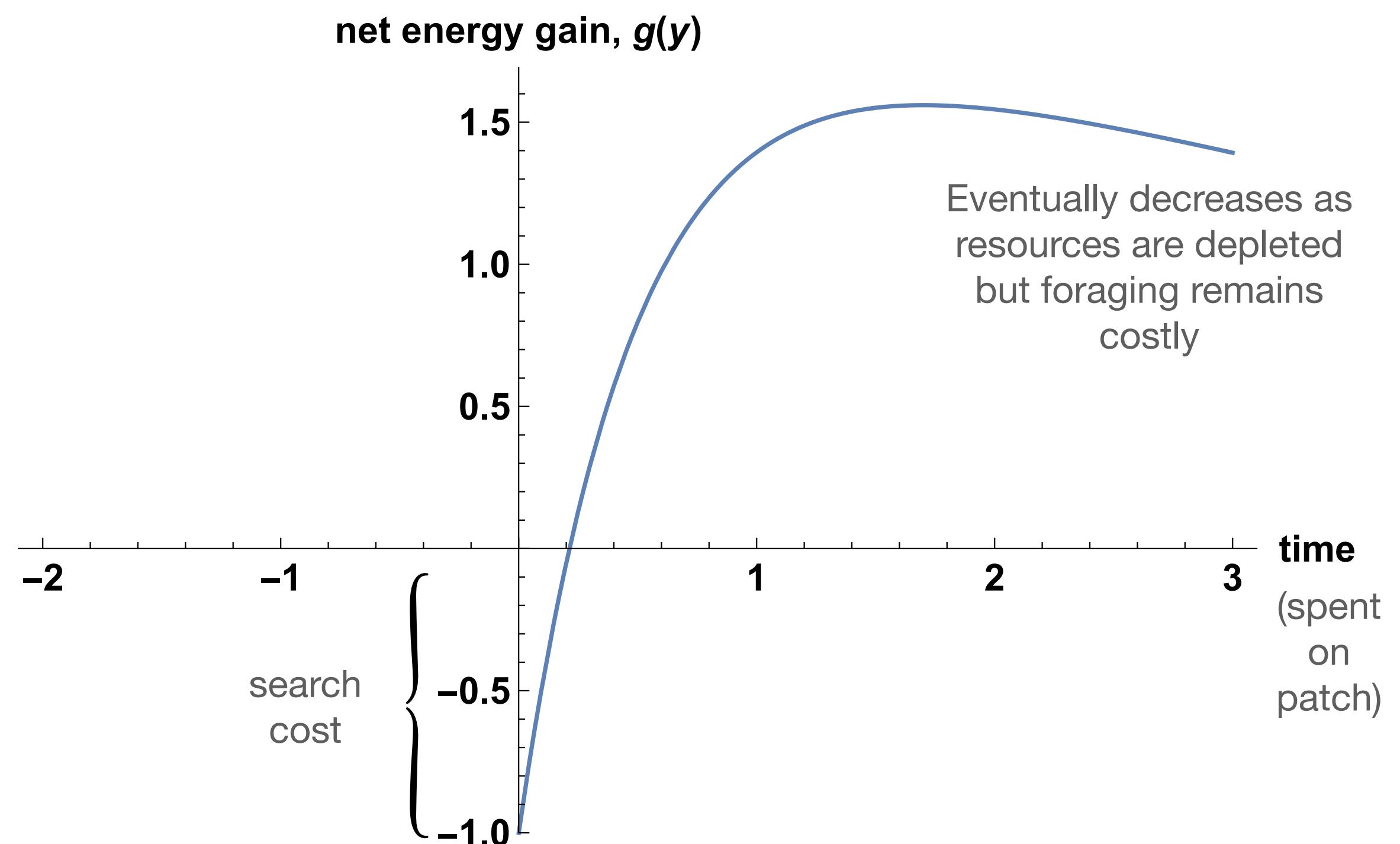
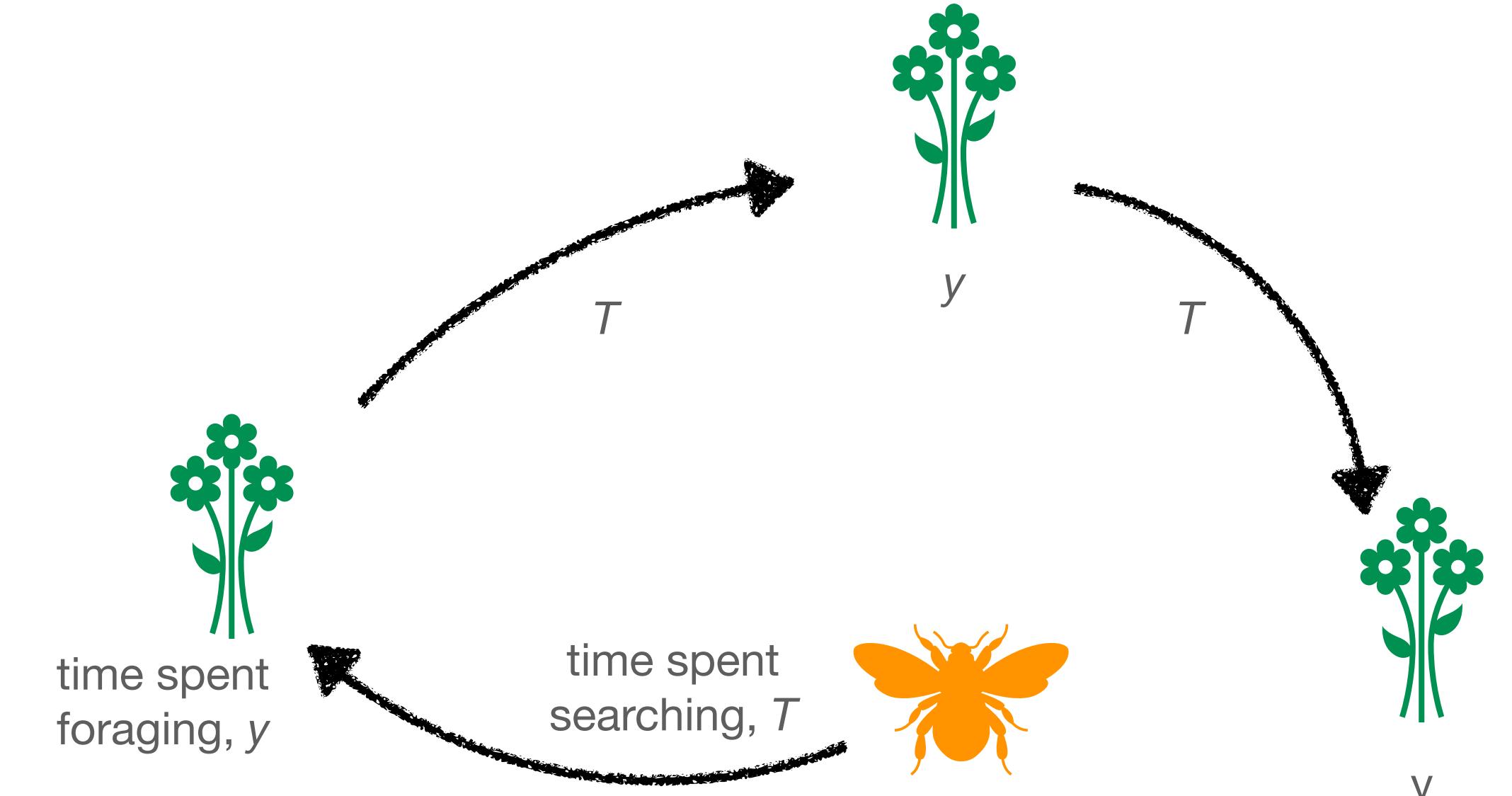
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- Selection gradient :

$$s(x) \propto \frac{g'(x)}{x + T} - \frac{g(x)}{(x + T)^2}$$

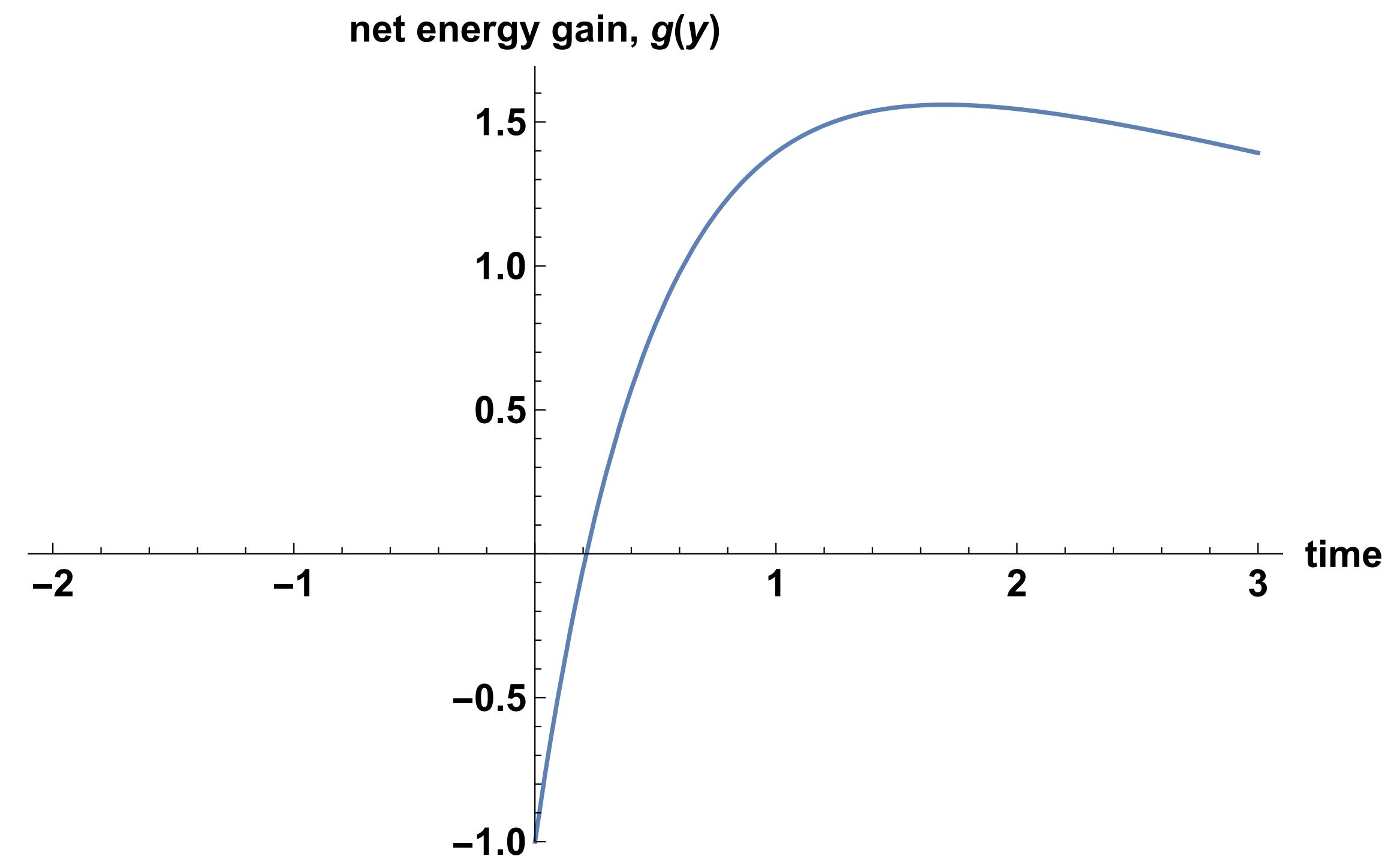
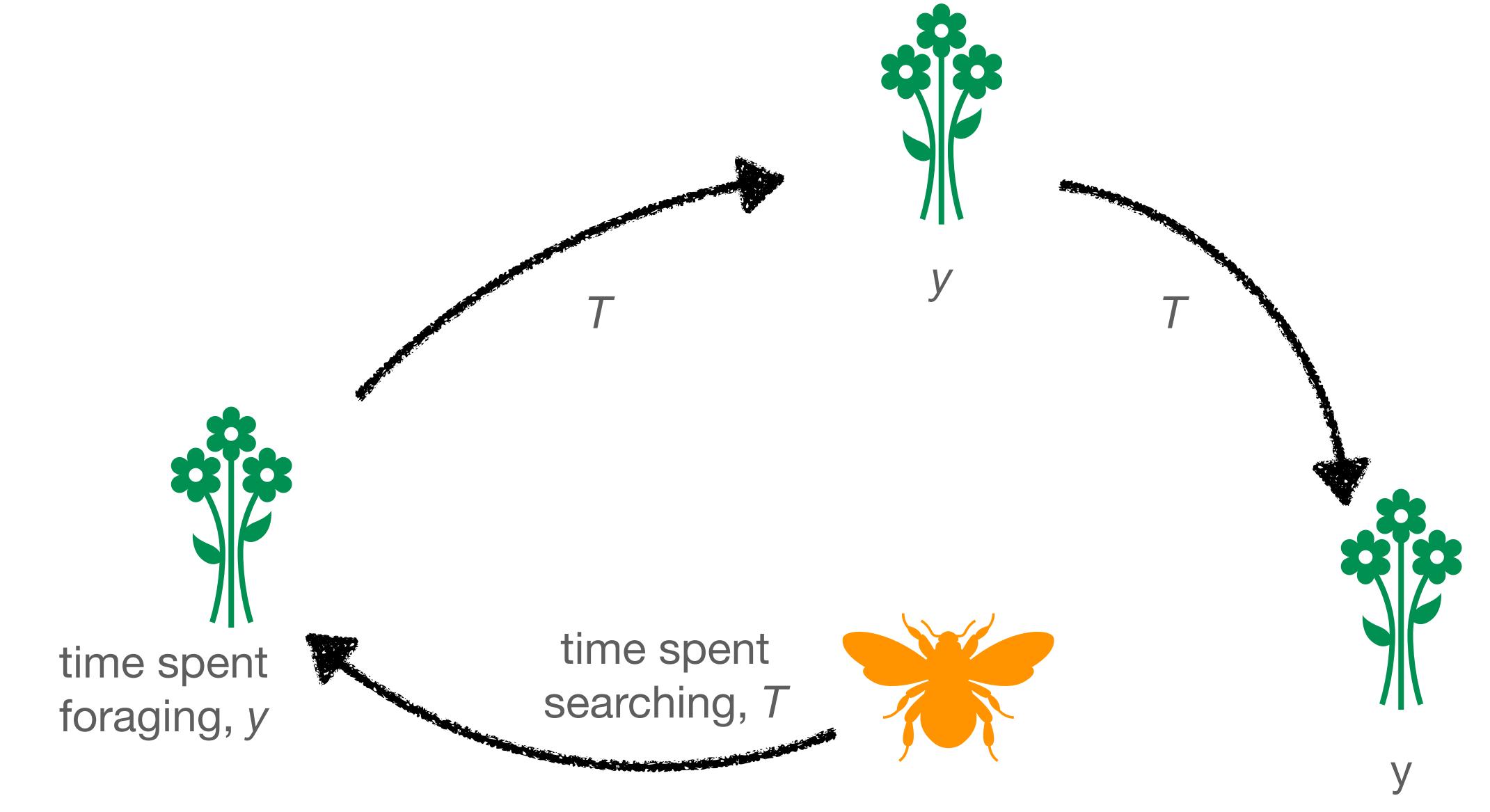


# Marginal value theorem

Optimum  $x^*$  such that  $s(x^*) = 0$ ,

i.e., such that

$$g'(x^*) = \frac{g(x^*)}{x^* + T} = R(x^*)$$

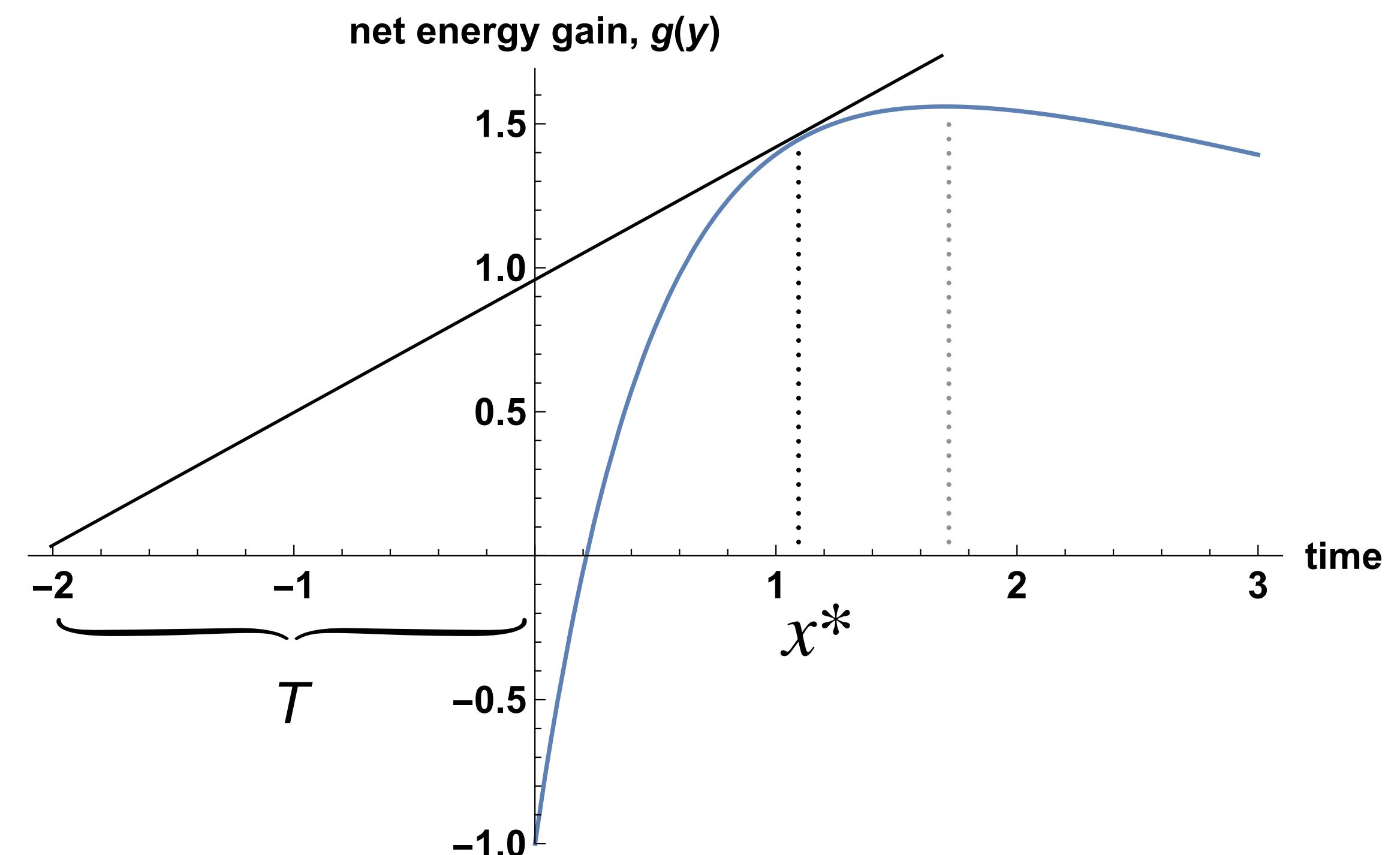
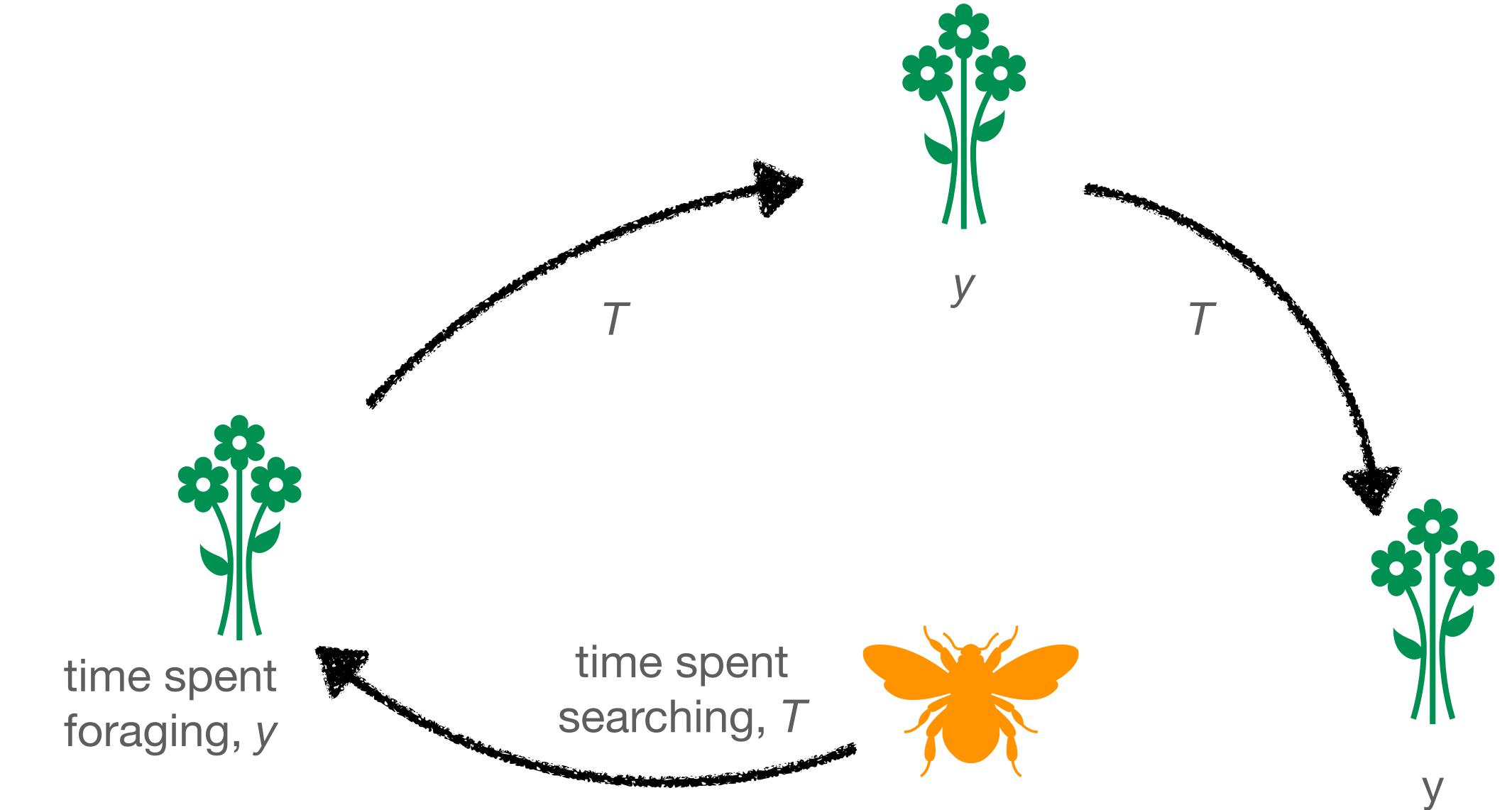


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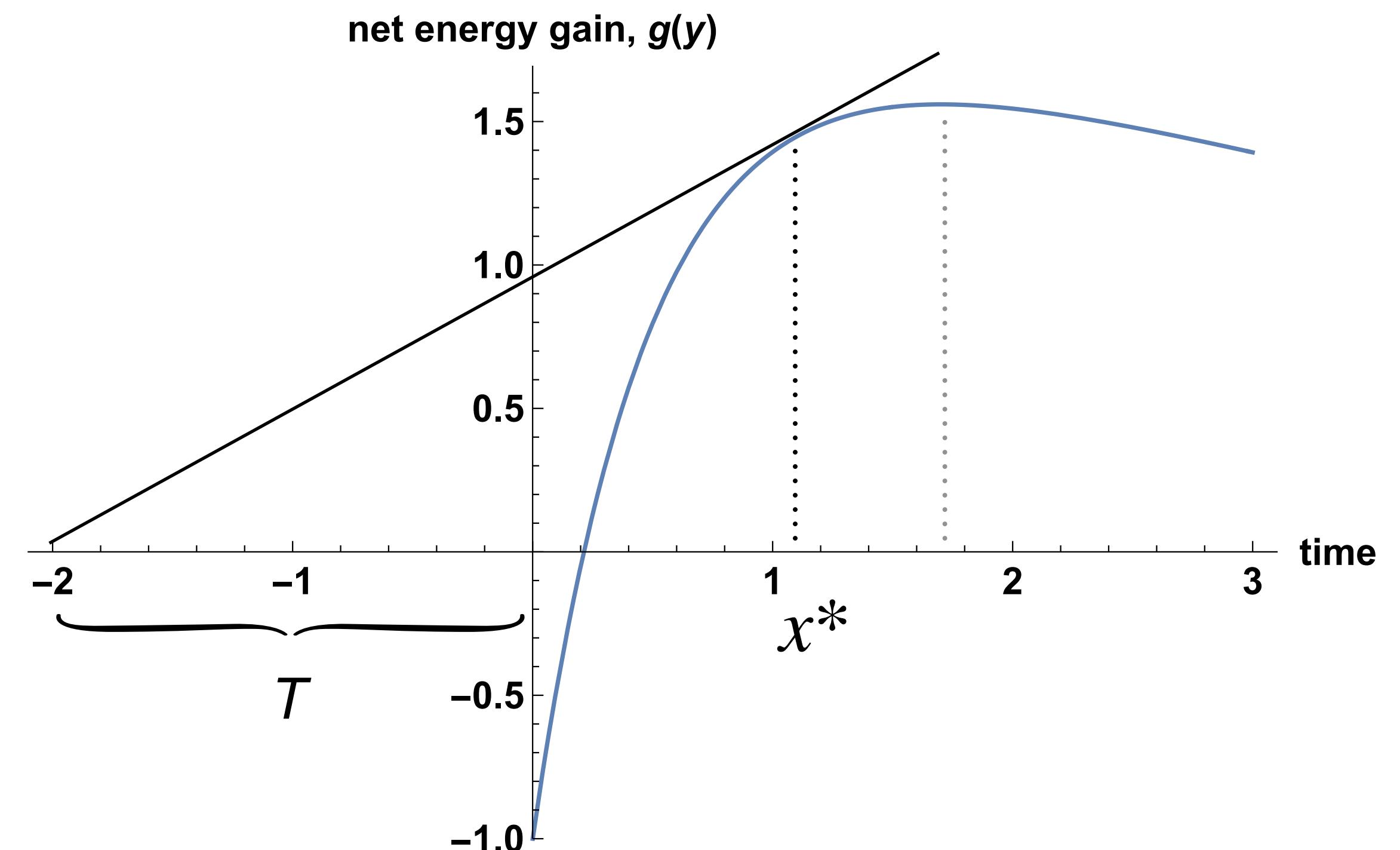
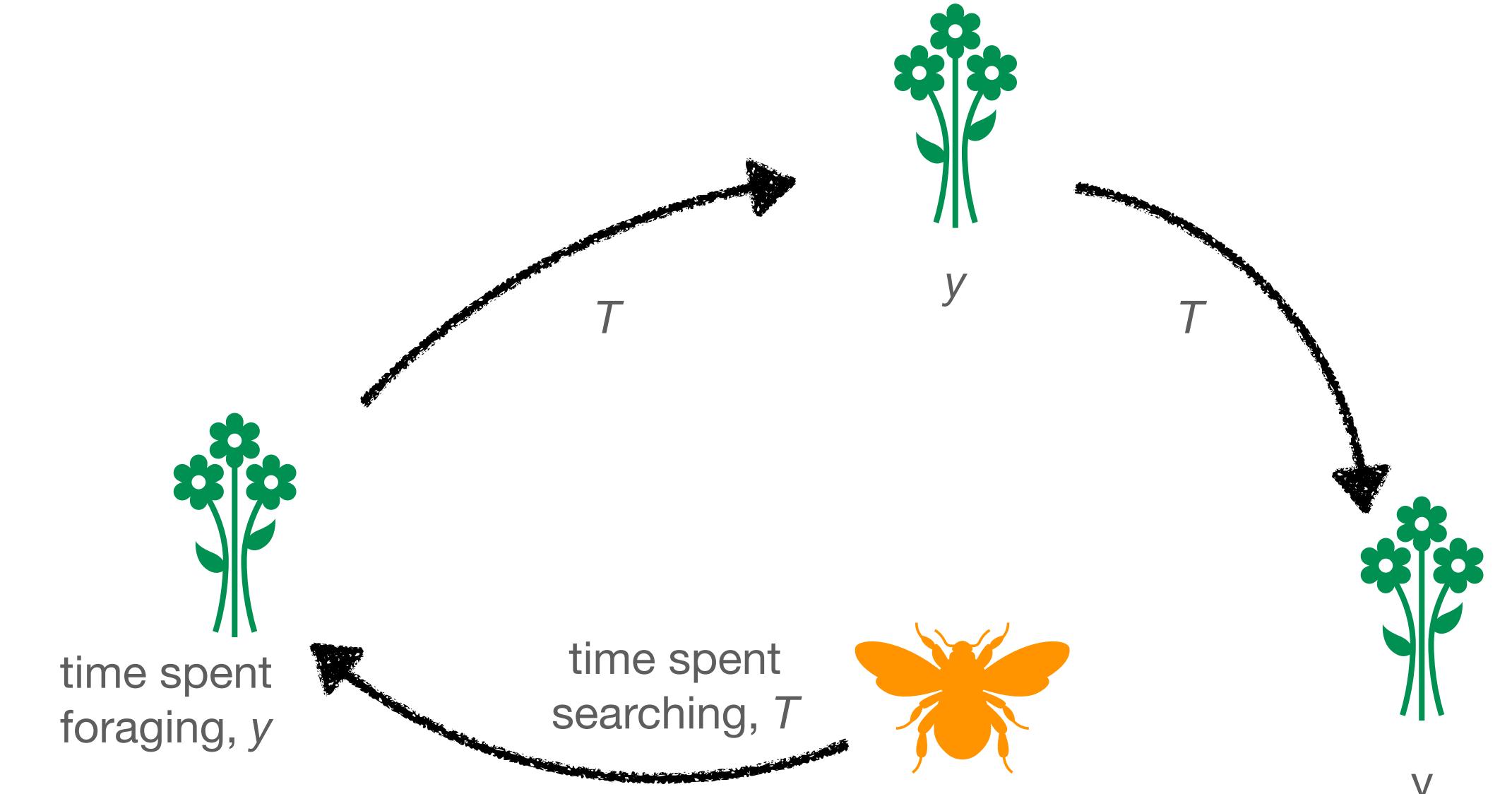
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An animal should leave when the marginal (or instantaneous) rate of energy gain  $g'(x^*)$  has fallen to the rate of energy gain  $R(x^*)$



# **When selection favours risky foraging?**

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## Variation in relationship with uncertainty



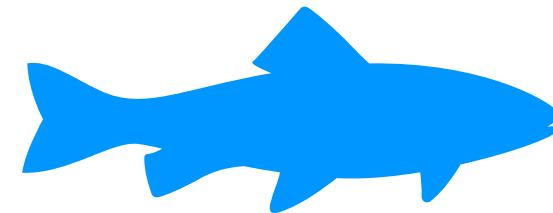
# **When selection favours risky foraging?**

## **State-dependent payoffs and uncertainty**

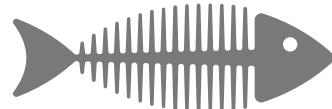
# When selection favours risky foraging?

## State-dependent payoffs and uncertainty

**High condition**  
e.g., well-fed



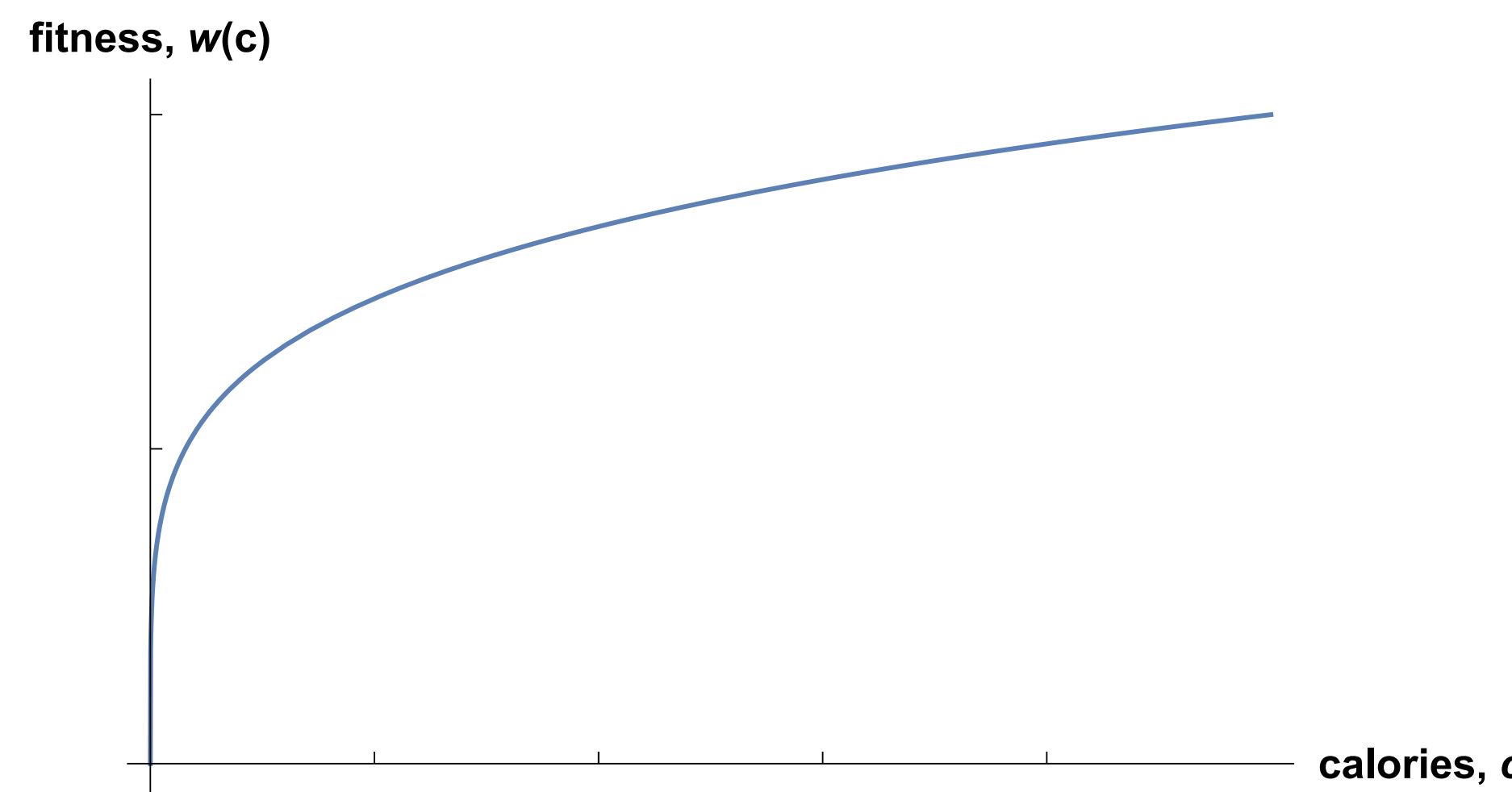
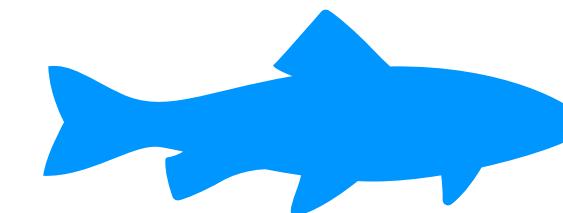
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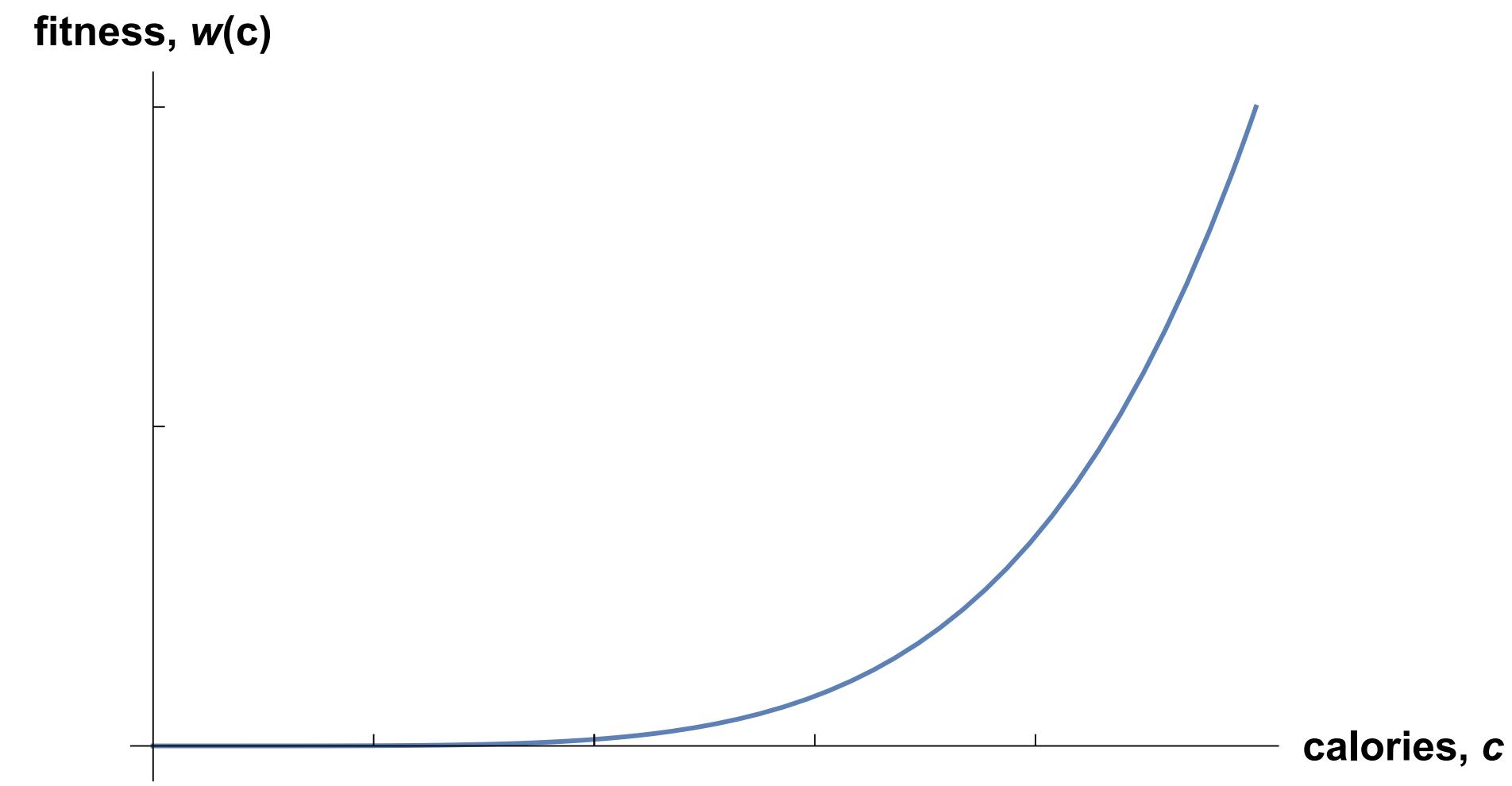
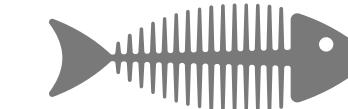
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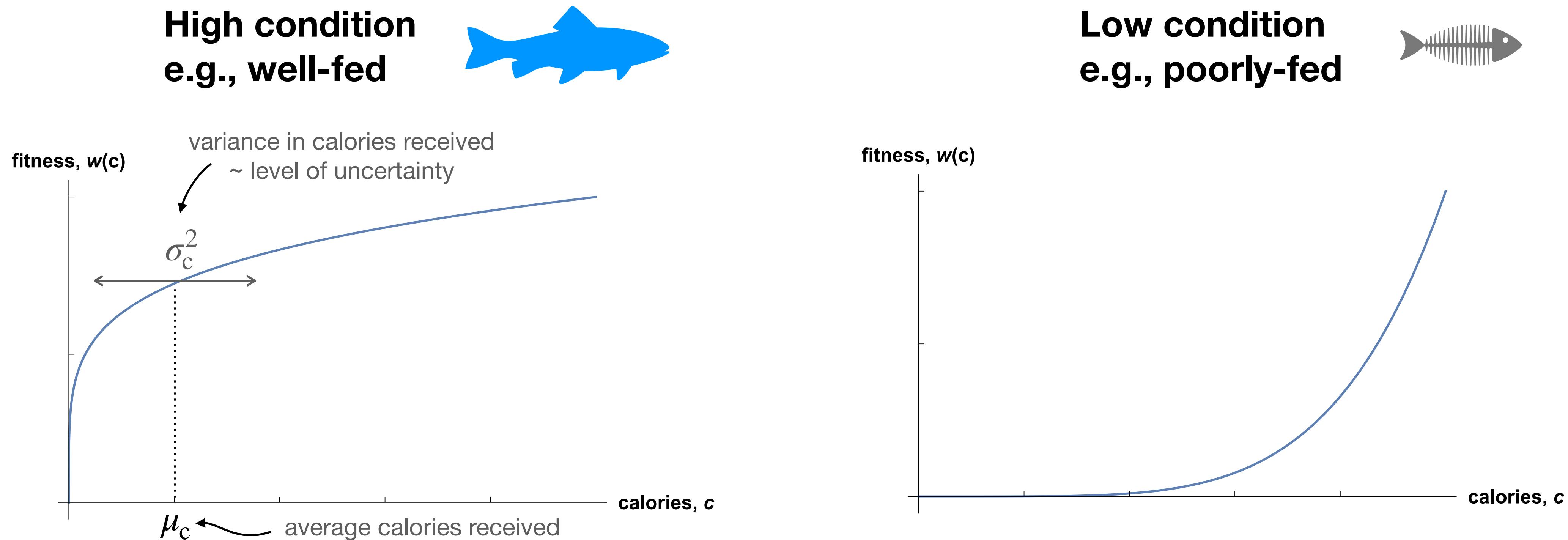


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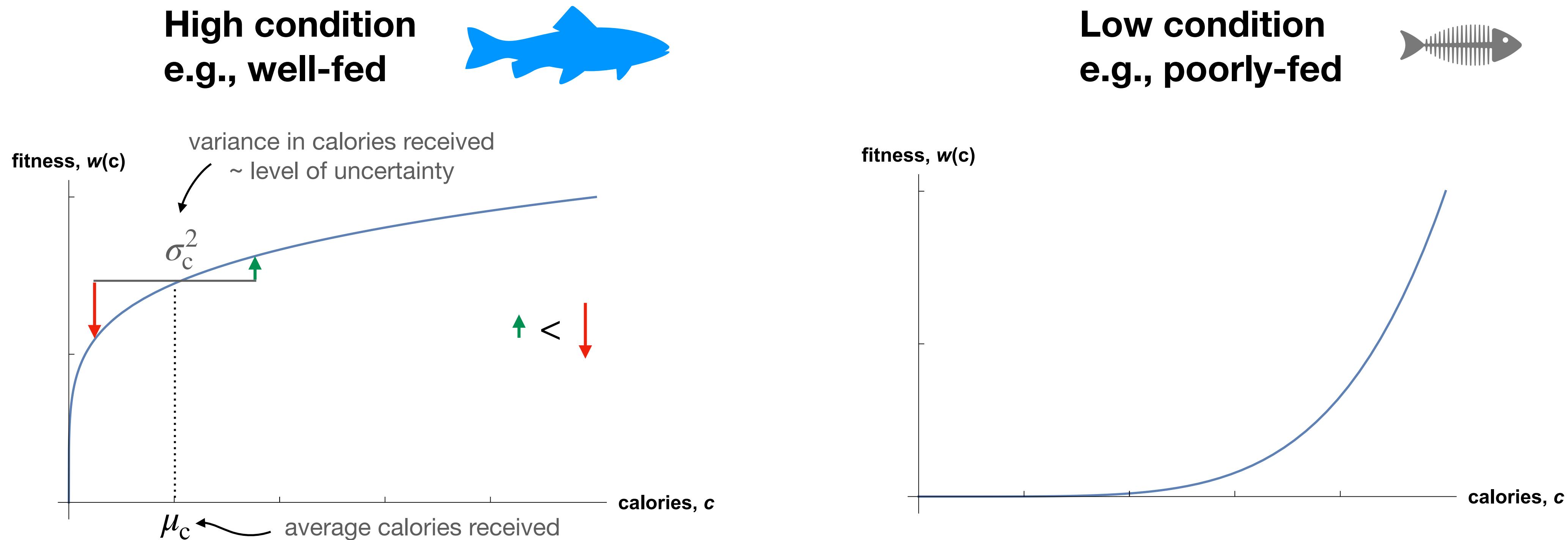
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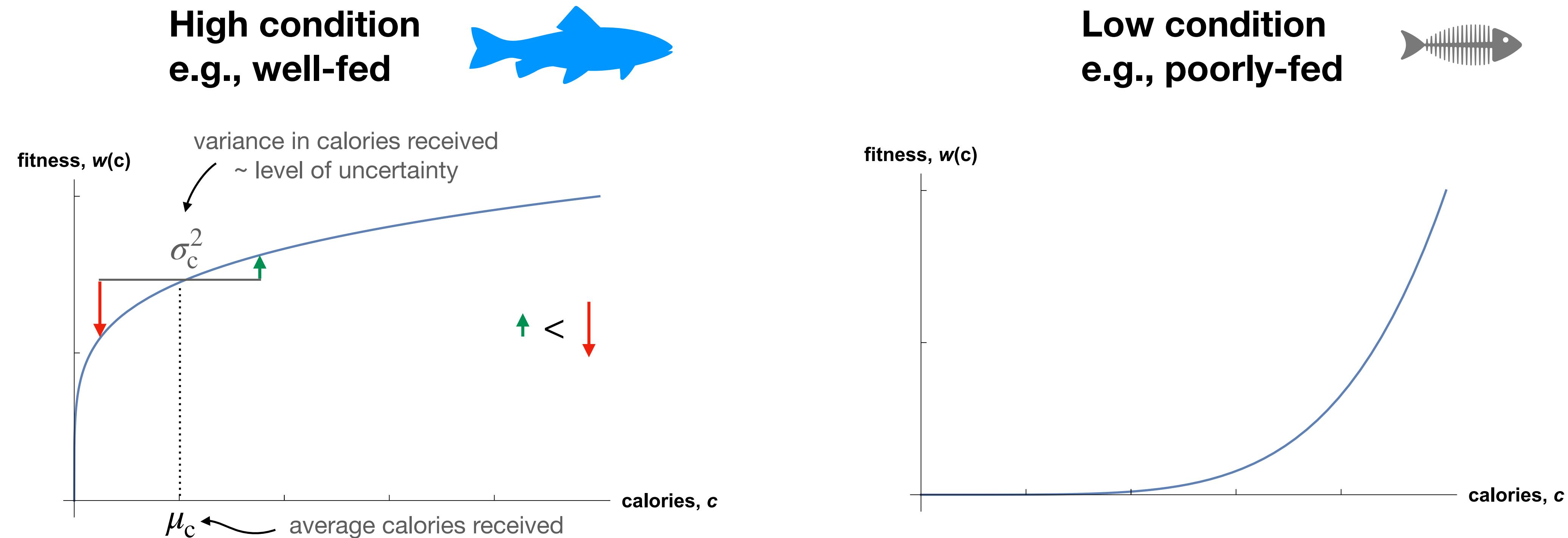
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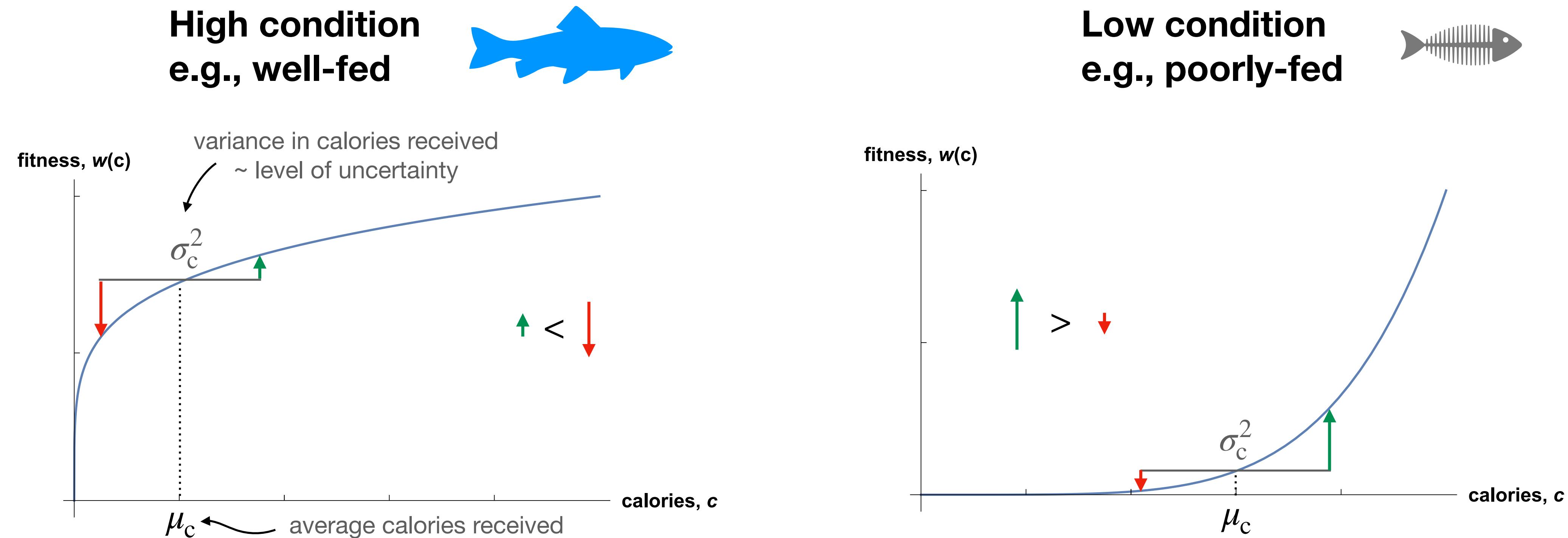
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Risk not worth taking: fitness cost of bad times  
outweighs fitness benefits of good times

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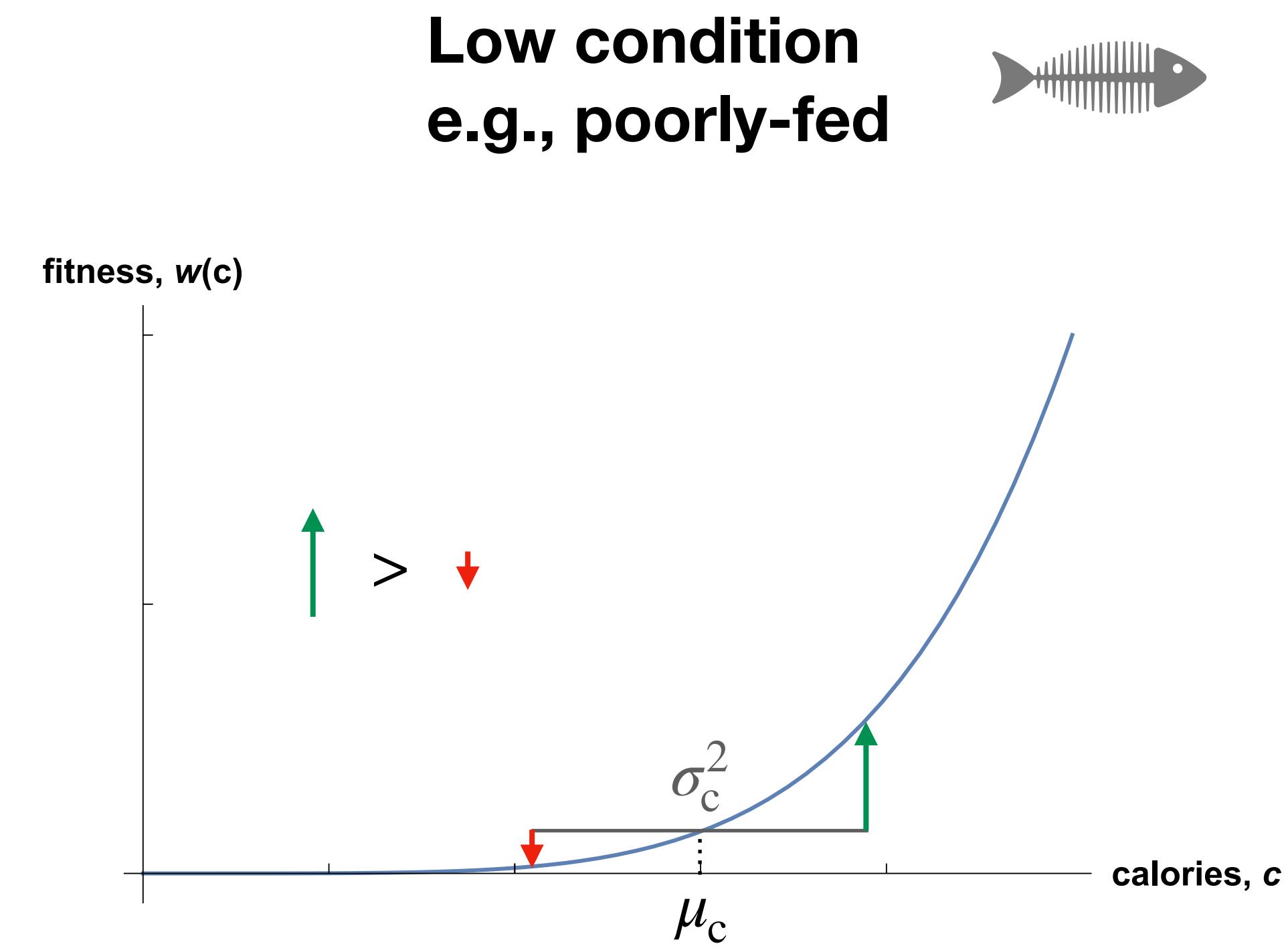
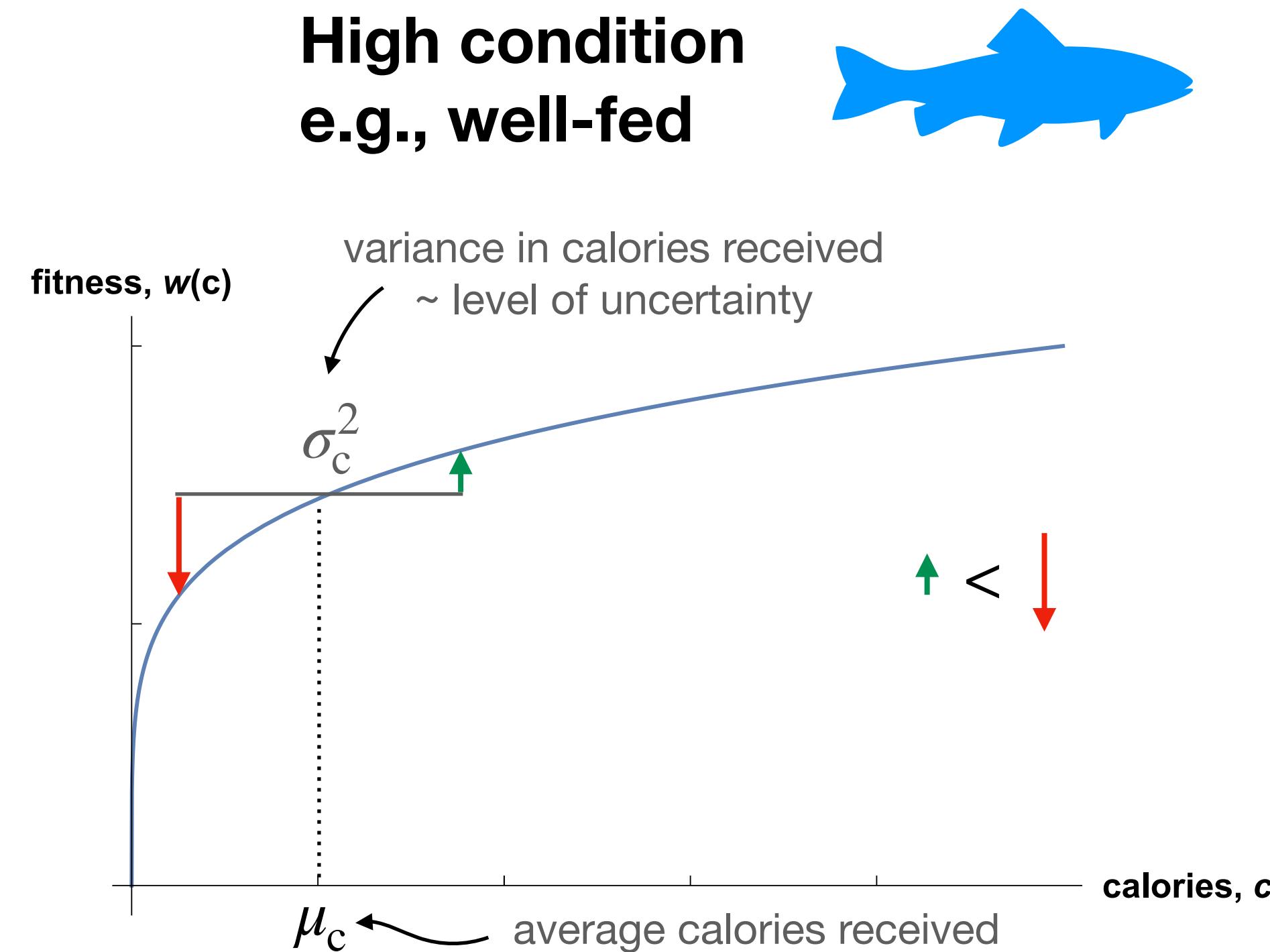
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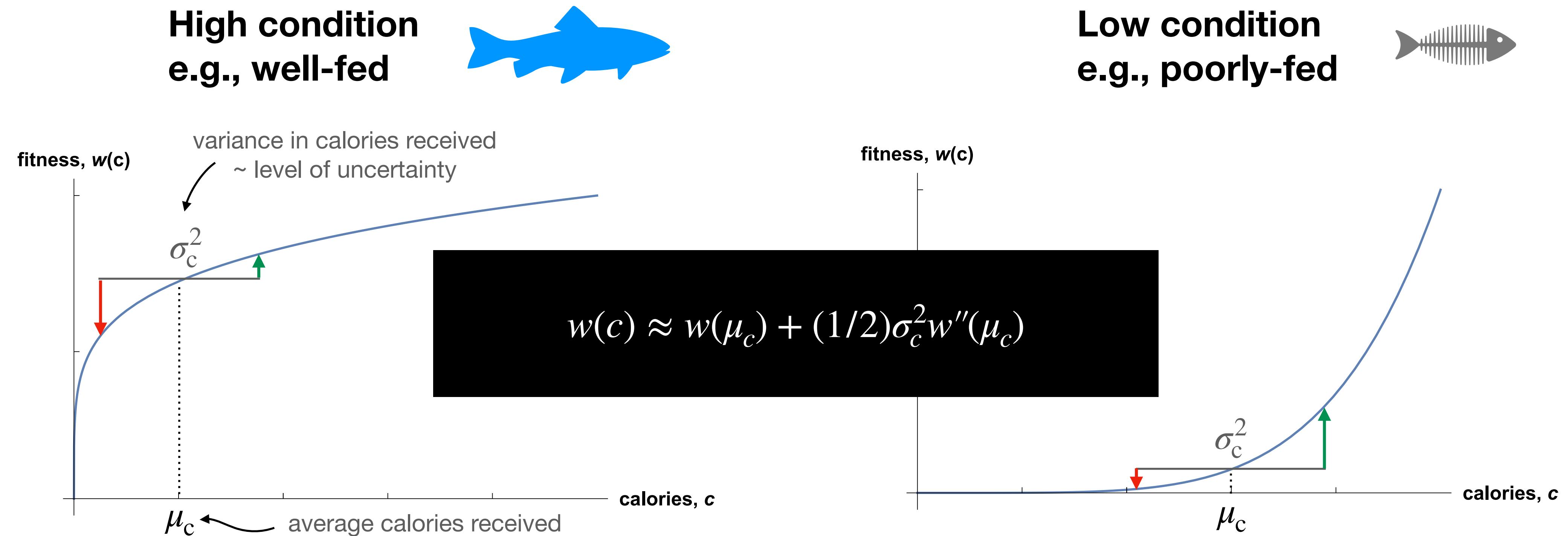


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# **The exploitation of renewable resources**

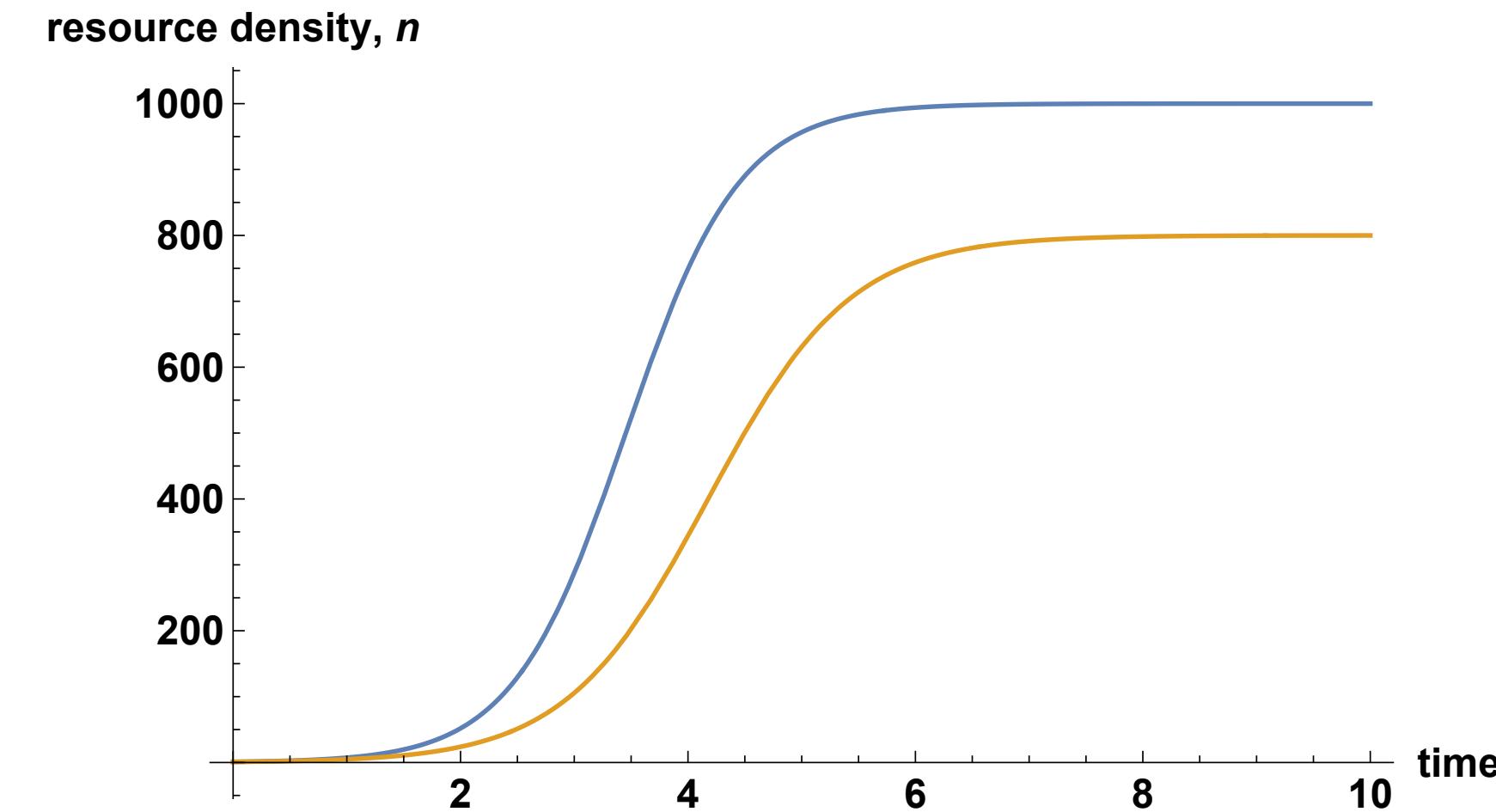
# The exploitation of renewable resources

## Schaefer's model

- Biotic resource with density  $n$ ,

$$\frac{dn}{dt} = \underbrace{r \left(1 - \frac{n}{K}\right)}_{\text{logistic growth}} n - \underbrace{n_c h(x) n}_{\text{harvesting by population of } n_c \text{ consumers with foraging effort } x}$$

foraging function



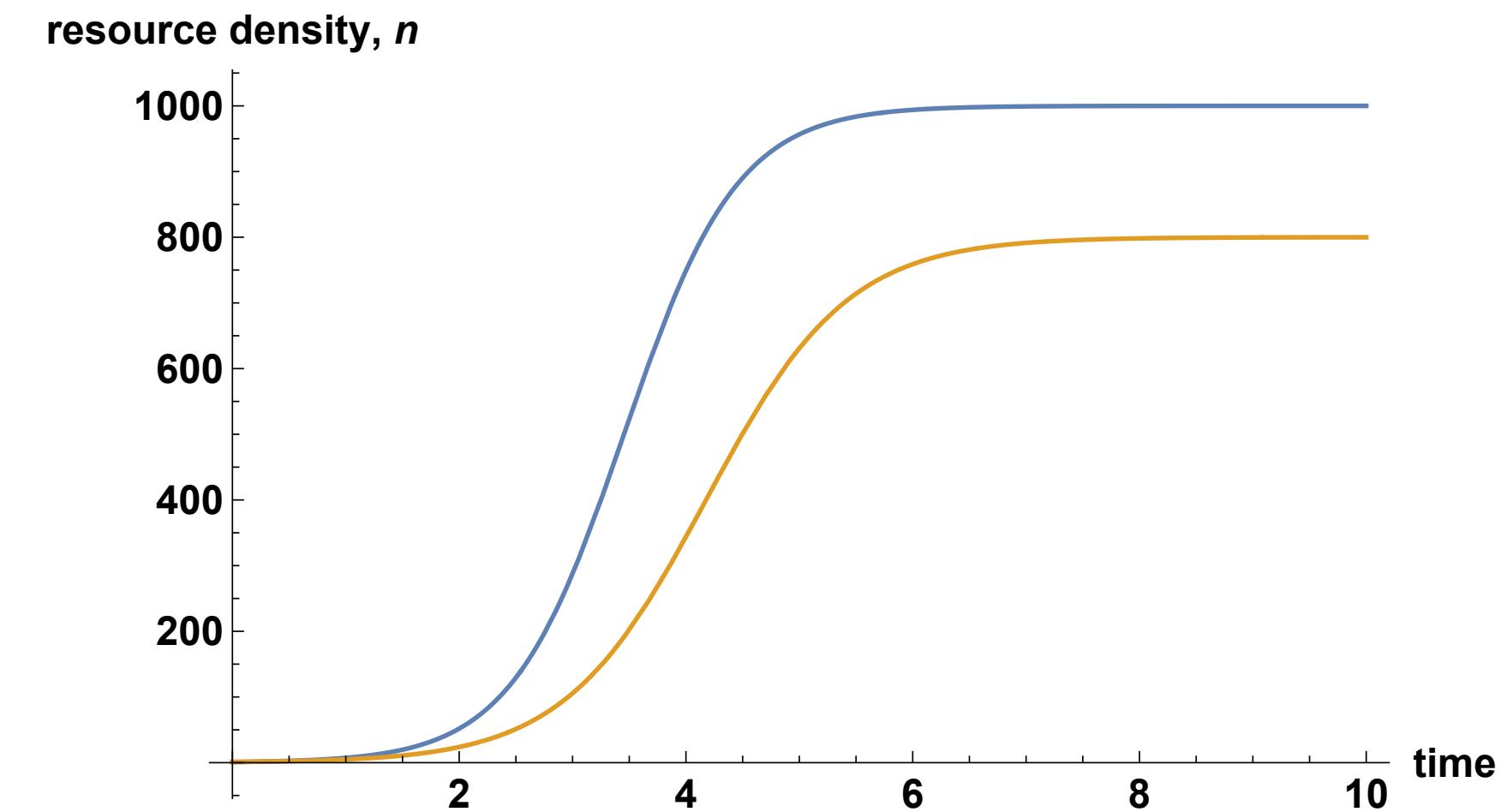
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$$\hat{n}(x) = K \left(1 - n_c \frac{h(x)}{r}\right)$$

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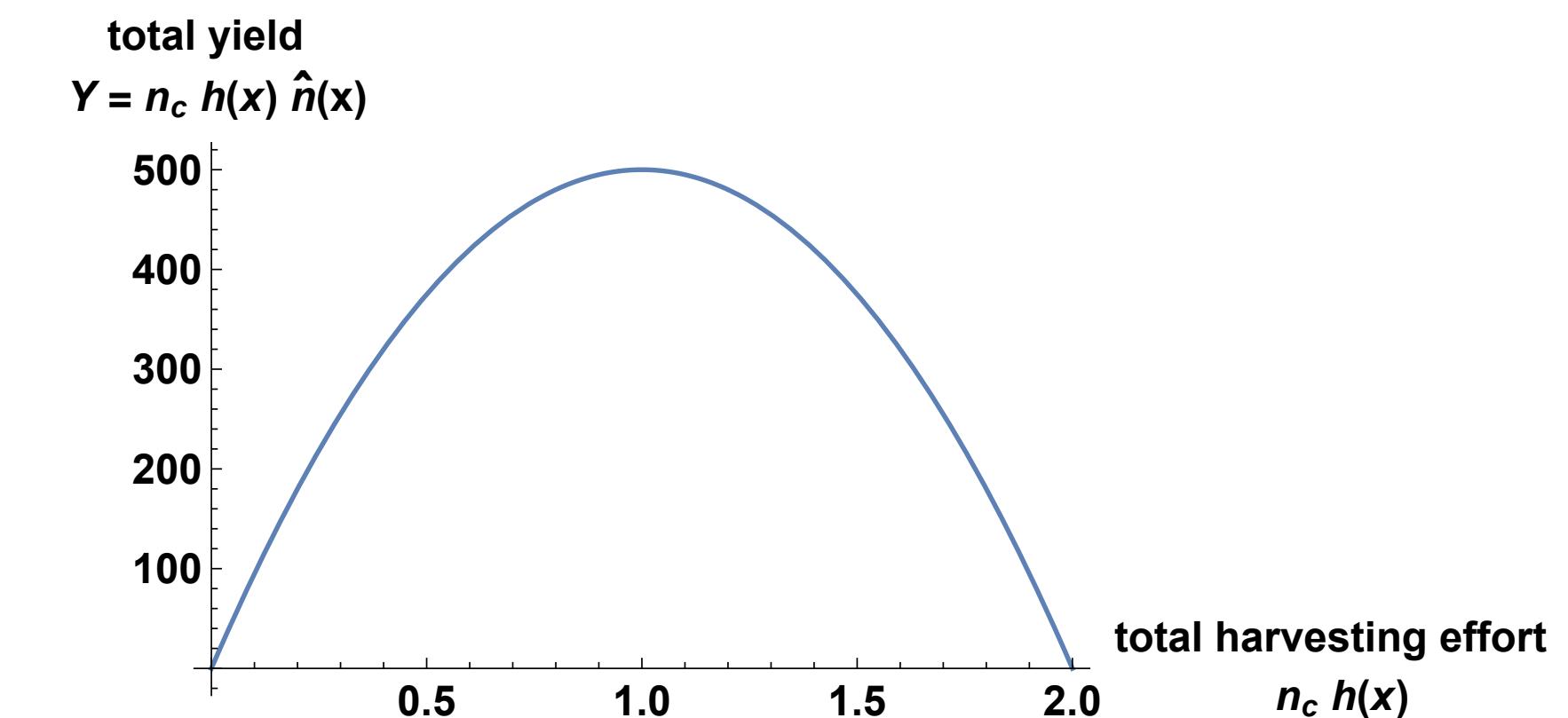
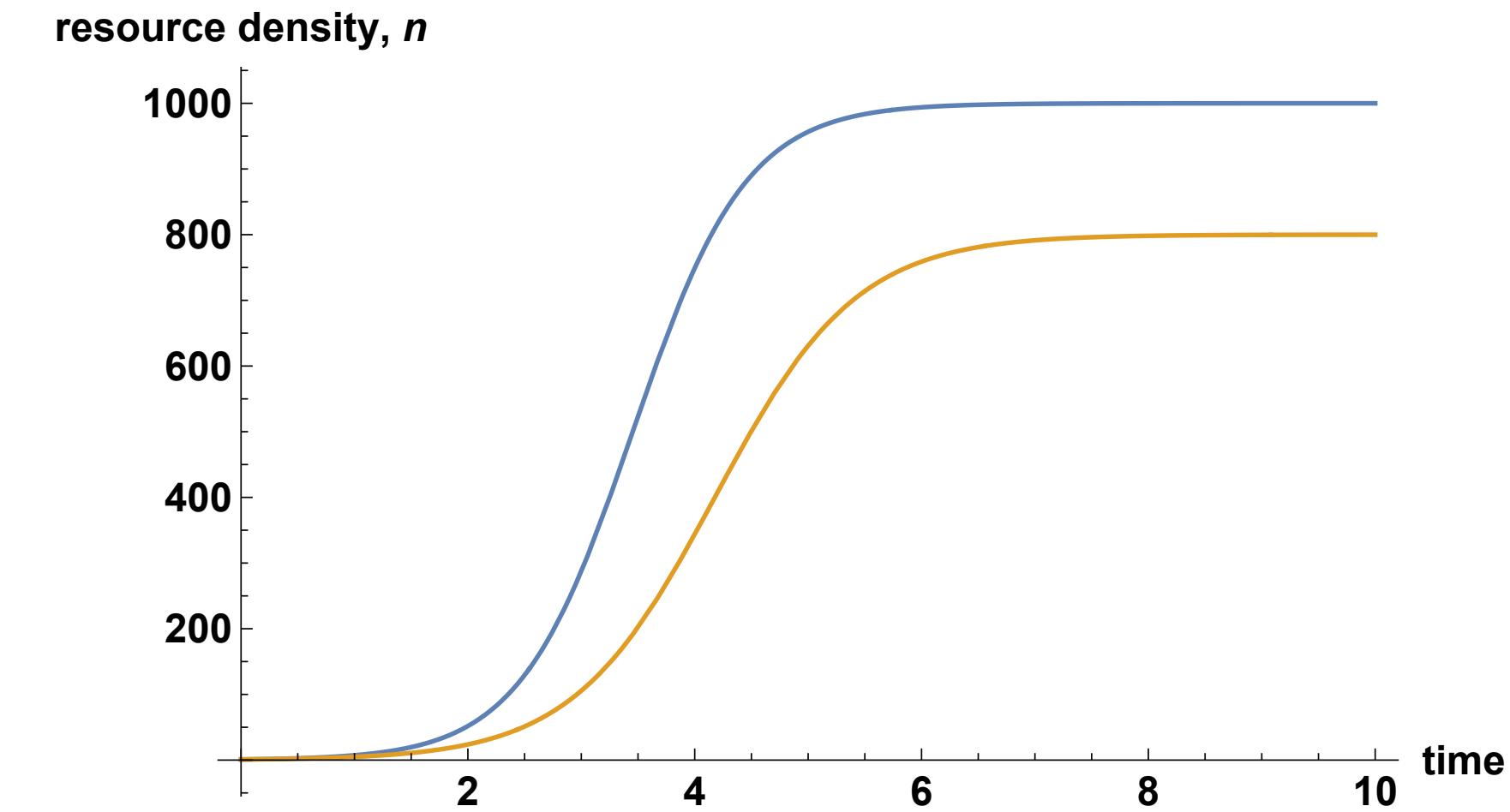
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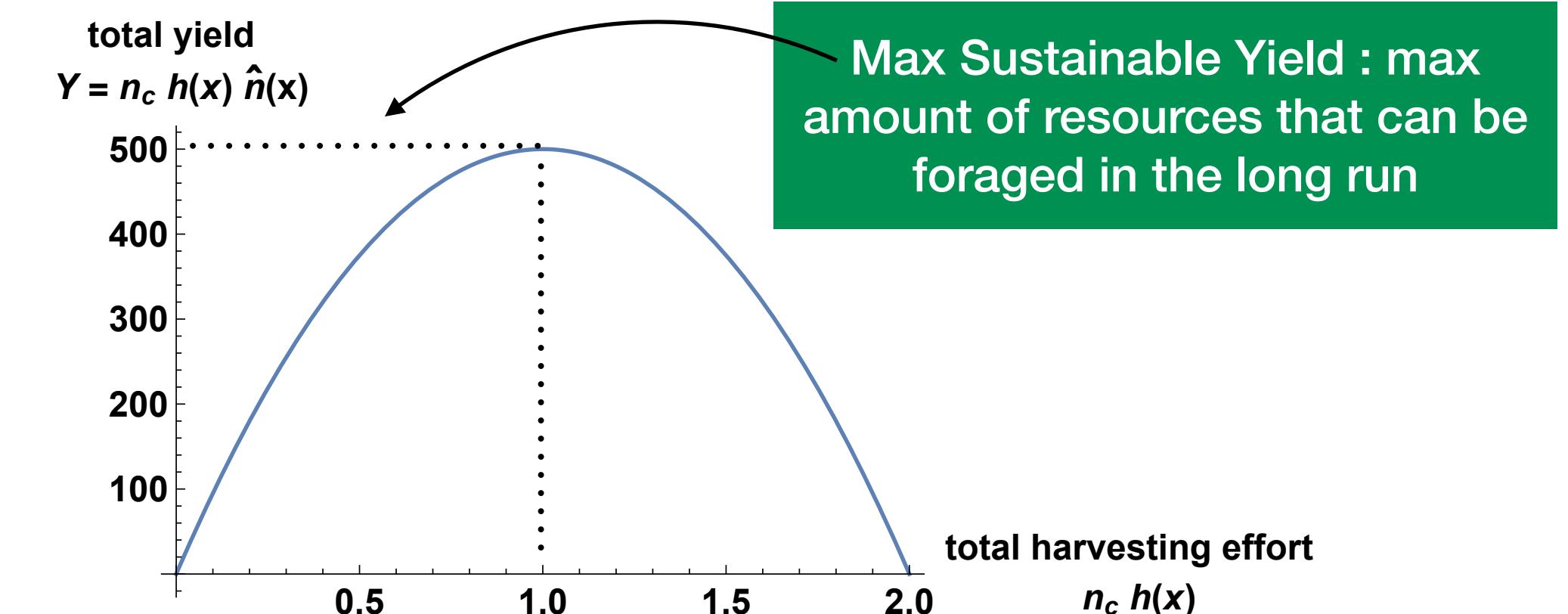
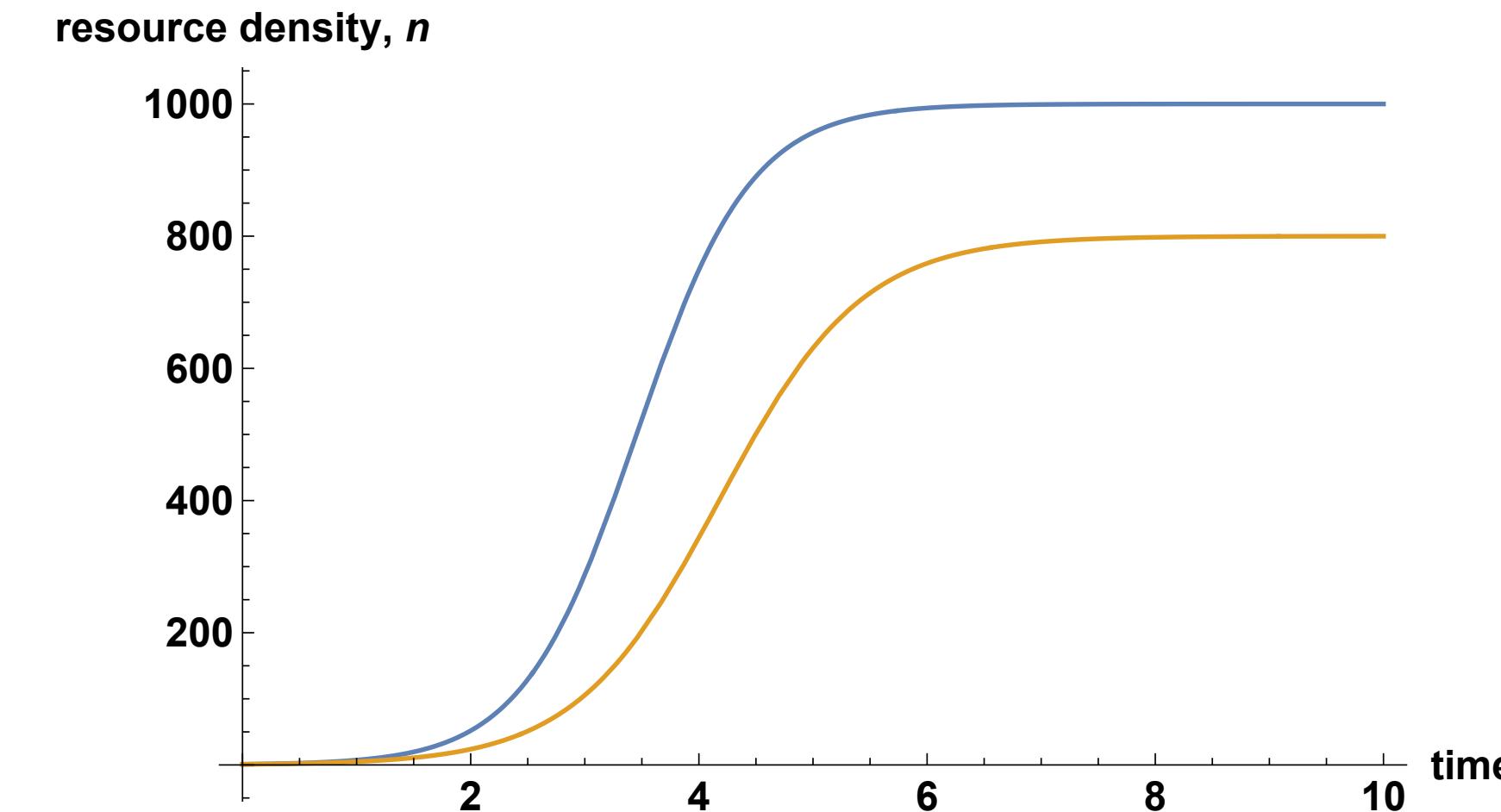
logistic growth

foraging function

harvesting by population  
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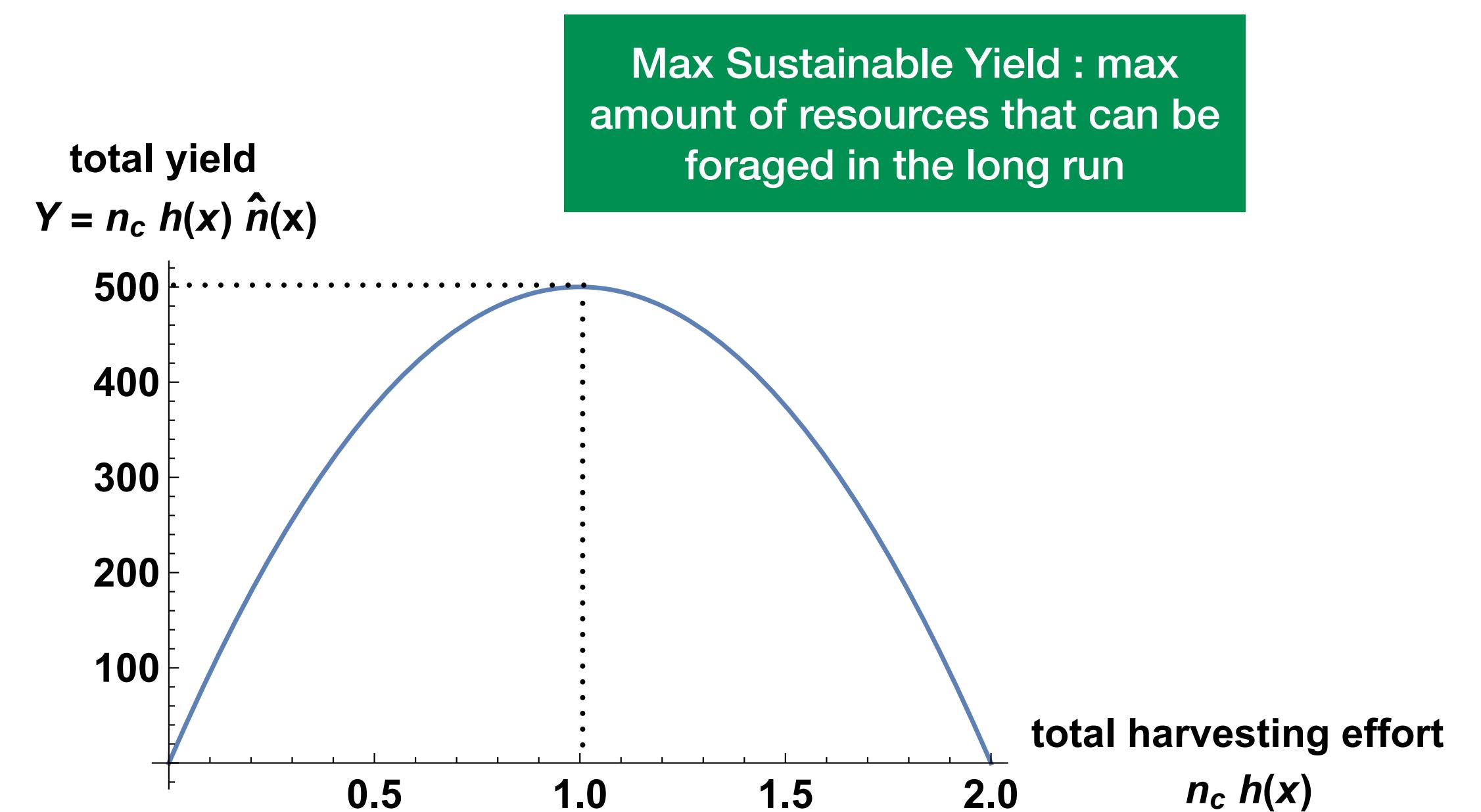
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## MSY and over-consumption

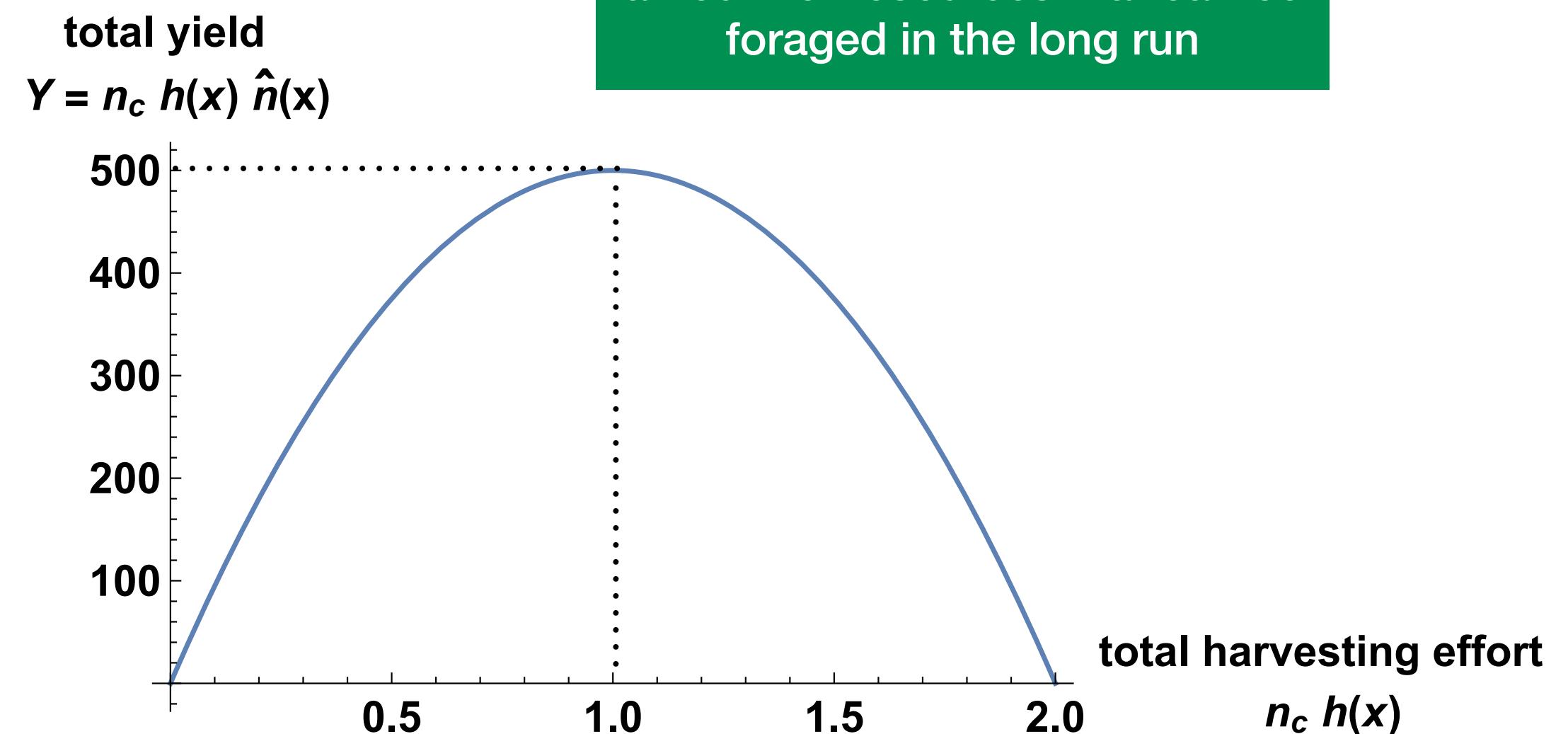


# The exploitation of renewable resources

## MSY and over-consumption

$$\text{Total yield} = n_c h(x) \times \hat{n}(x) = n_c x \times K \left( 1 - n_c \frac{x}{r} \right)$$

$h(x) = x$

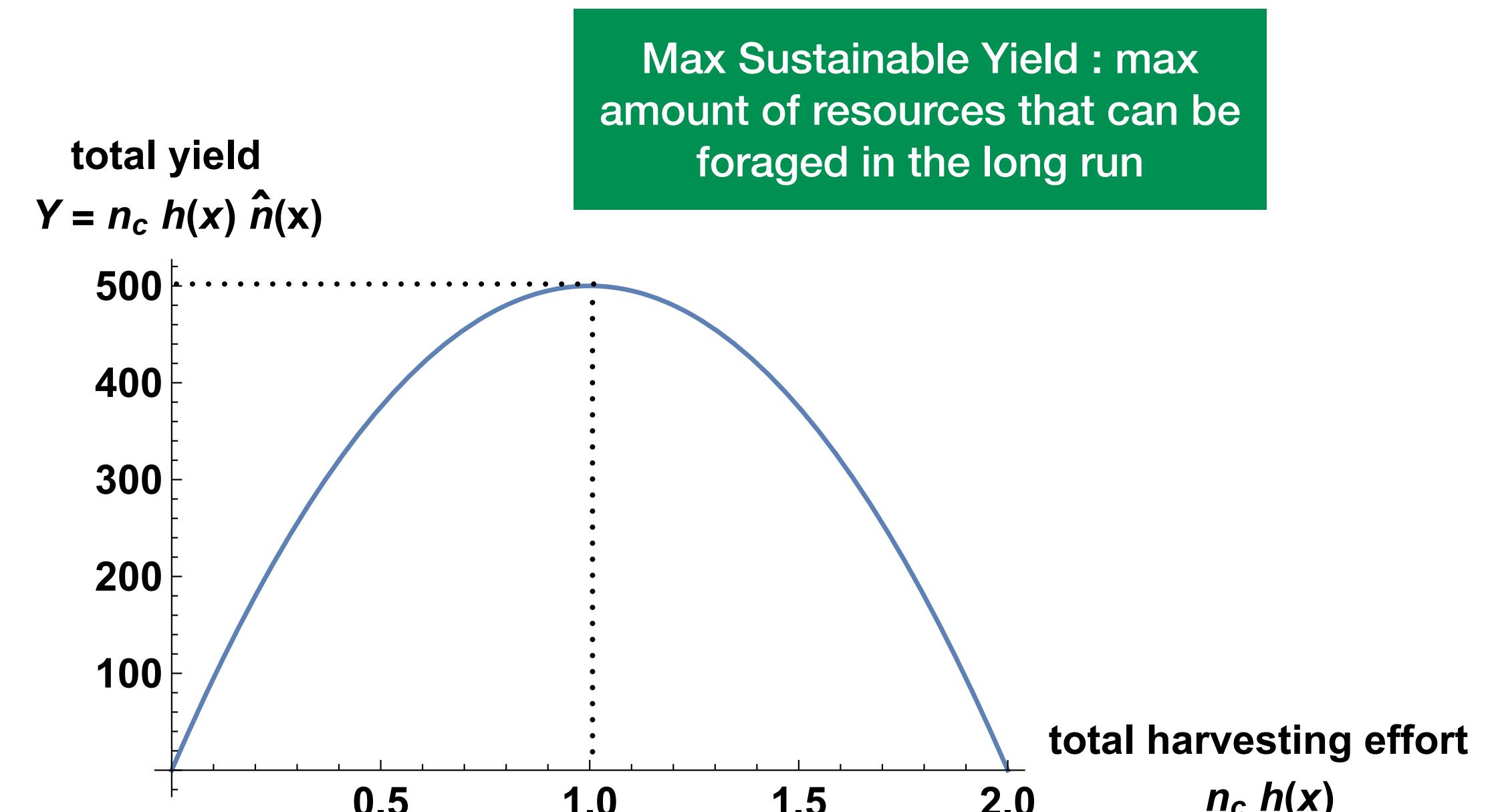


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- Total yield =  $n_c h(x) \times \hat{n}(x) = n_c x \times K \left( 1 - n_c \frac{x}{r} \right)$
- $x_{MSY}$ : Foraging effort that maximises total yield =  

$$x_{MSY} = \frac{1}{n_c} \frac{r}{2}$$
- MSY =  $n_c h(x_{MSY}) \times \hat{n}(x_{MSY}) = \frac{Kr}{4}$
- Resource density =  $\hat{n}(x_{MSY}) = \frac{K}{2}$



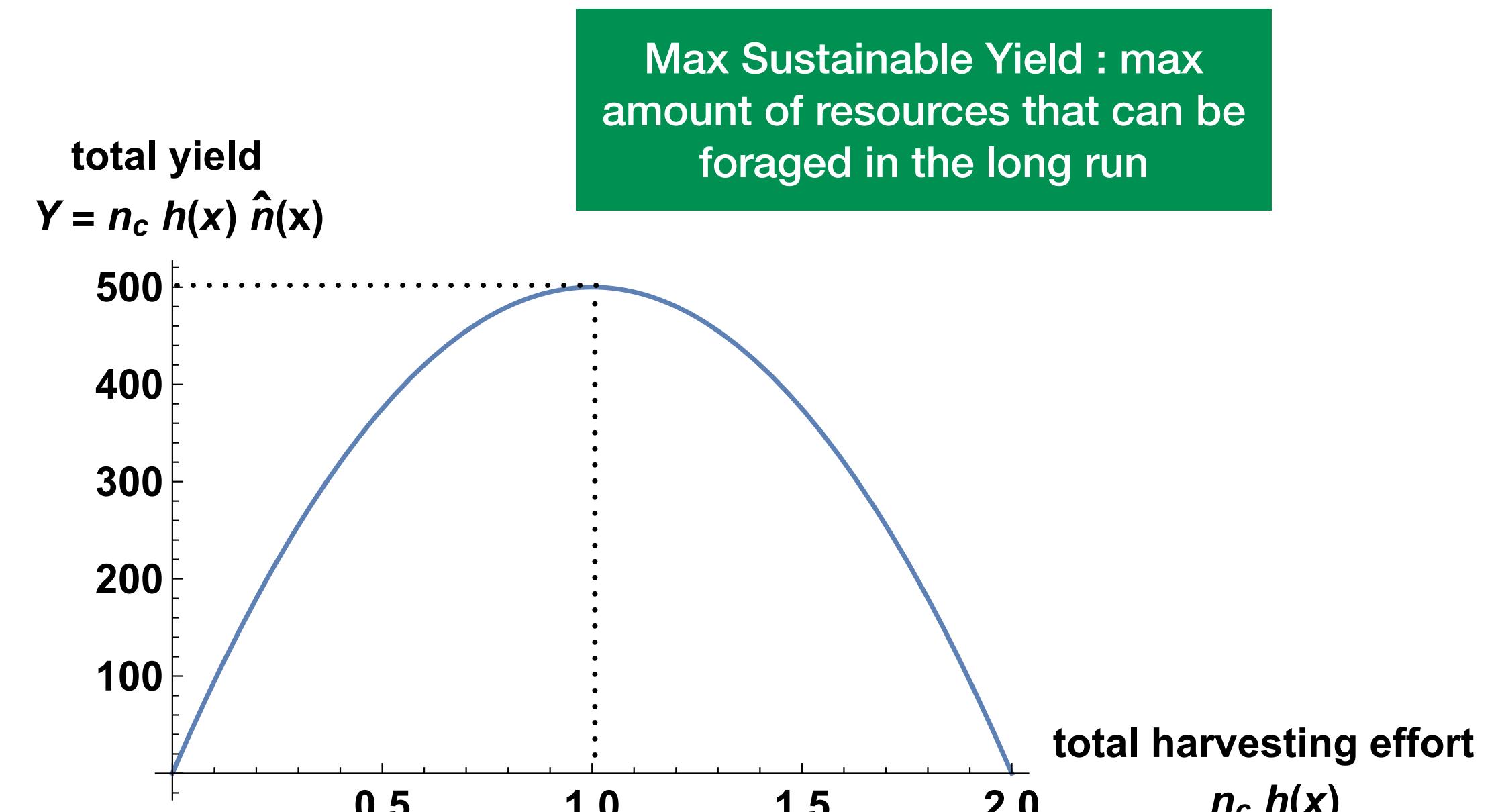
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- Any effort above  $x_{MSY}$  amounts to over-exploitation.



# **The exploitation of renewable resources**

## **How evolution shapes foraging of biotic resources**

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- Fitness of a mutant with foraging effort  $y$  in a resident population  $x$ ,

individual yield - individual cost of effort

$$w(y, x) \propto y\hat{n}(x) - c(y)$$

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$$\bullet \quad x^* = x_{\text{MSY}} \frac{2Kn_c}{Kn_c + c_0 r} \quad \begin{aligned} h(x) &= x \\ c(x) &= \frac{c_0}{2}x^2 \end{aligned}$$

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$$h(x) = x$$

$$c(x) = \frac{c_0}{2}x^2$$

When cost is large,  $c_0 \geq \frac{Kn_c}{r}$  then  $x^* \leq x_{\text{MSY}}$ .  
Otherwise,  $x^* > x_{\text{MSY}}$ .  
When  $c_0 = 0$ , evolution leads to resource extinction.

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Due to competition, evolution typically leads to over-exploitation and lower yield than if individuals were coordinated.

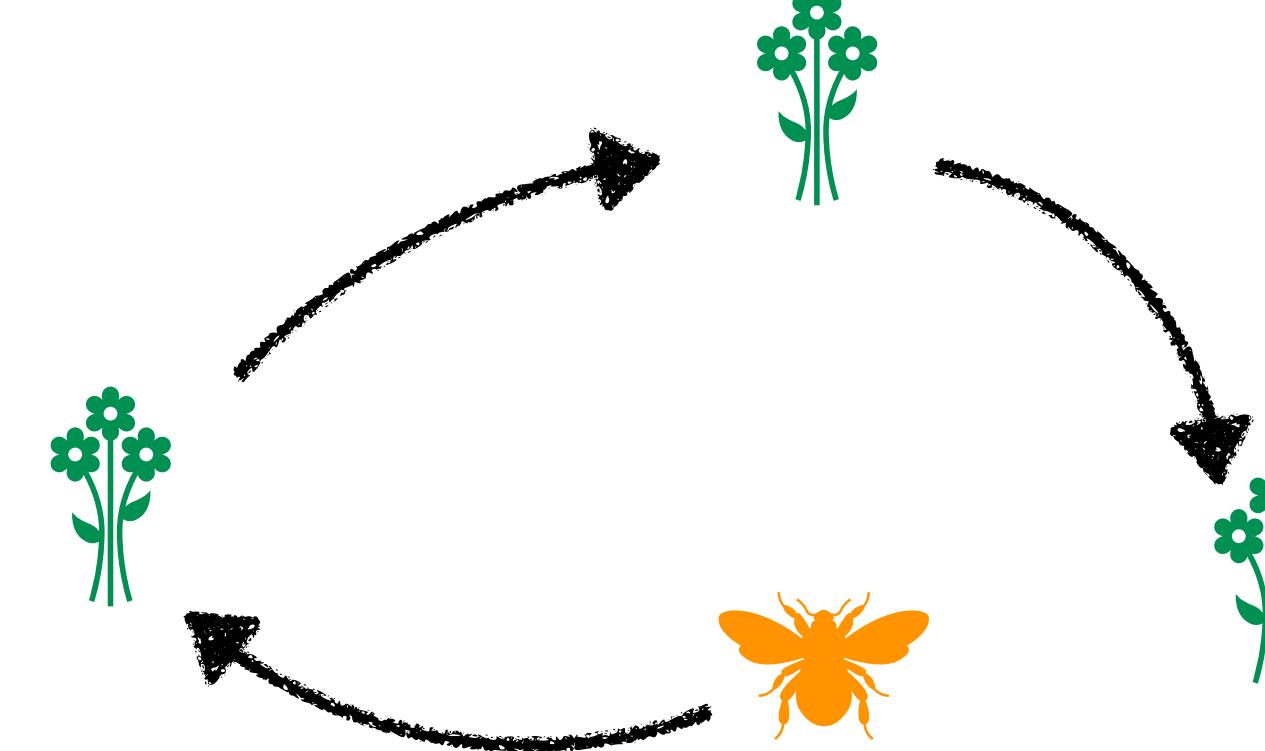
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# Summary



- Marginal value theorem allows to understand when an organism should leave for new pastures: leave when the *marginal* rate of energy gain has fallen to the total rate of gain.
- Risky foraging behaviours can be explained from state dependent payoffs where the fitness of low condition individuals accelerates with energy.
- For biotic resources, there may exist a foraging effort such that yield is maximised and resources are maintained. Due to competition, however, natural selection tends to favour over-consumption.

