Part III - Foraging theory

Sex, Ageing and Foraging Theory

resources

energy

offspring

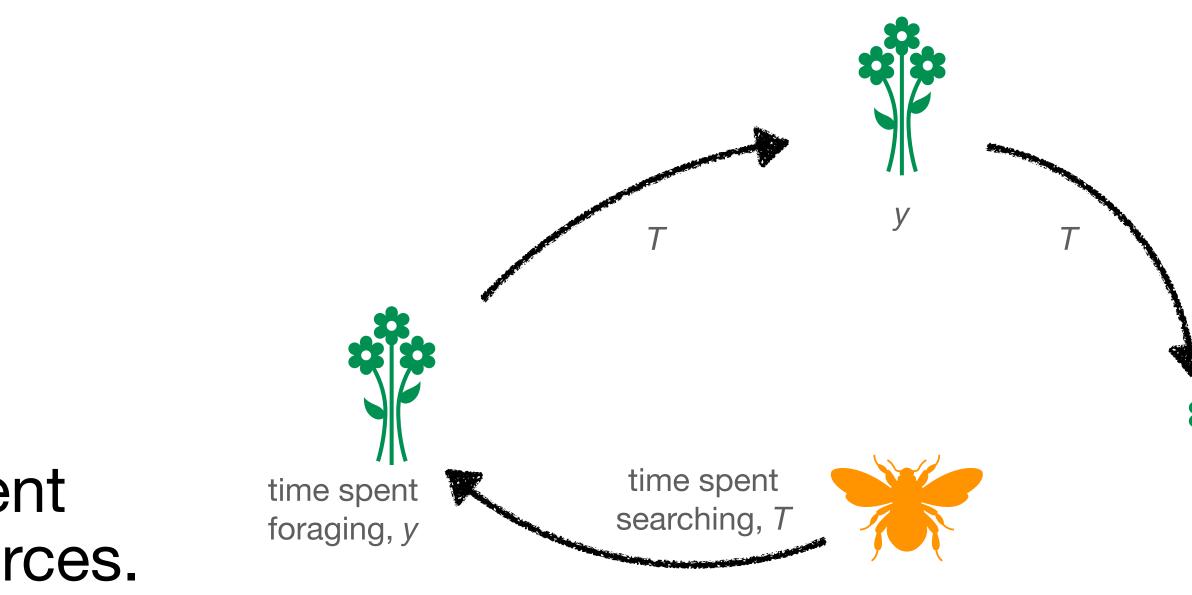
fitness



Today three topic in foraging theory

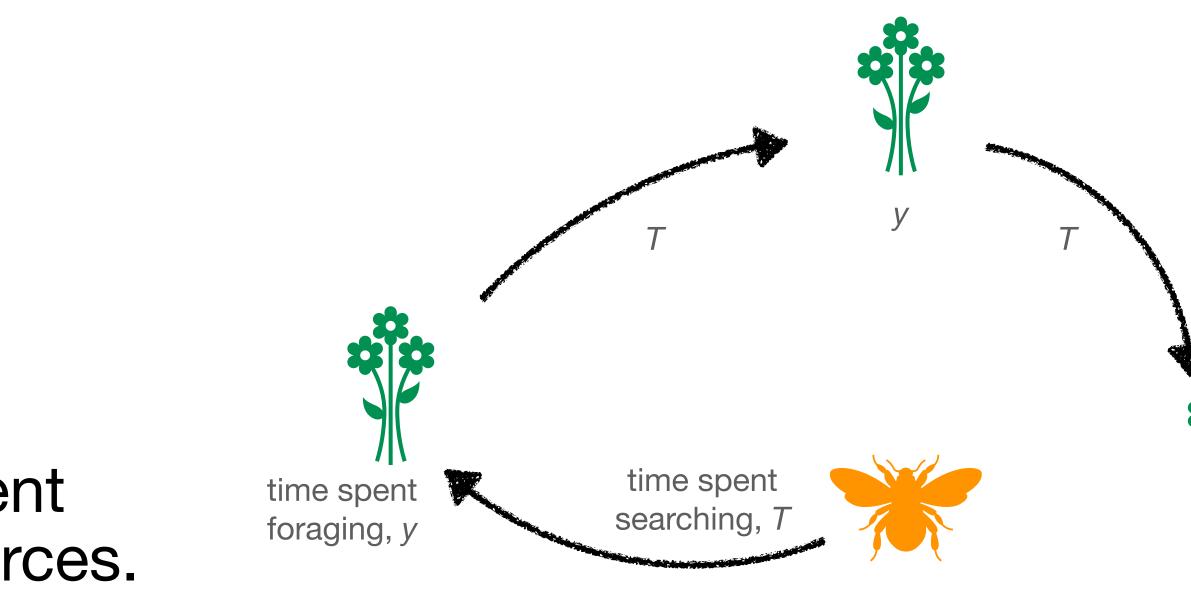
- Marginal Value theorem
- Risk taking
- Exploitation of natural resources

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



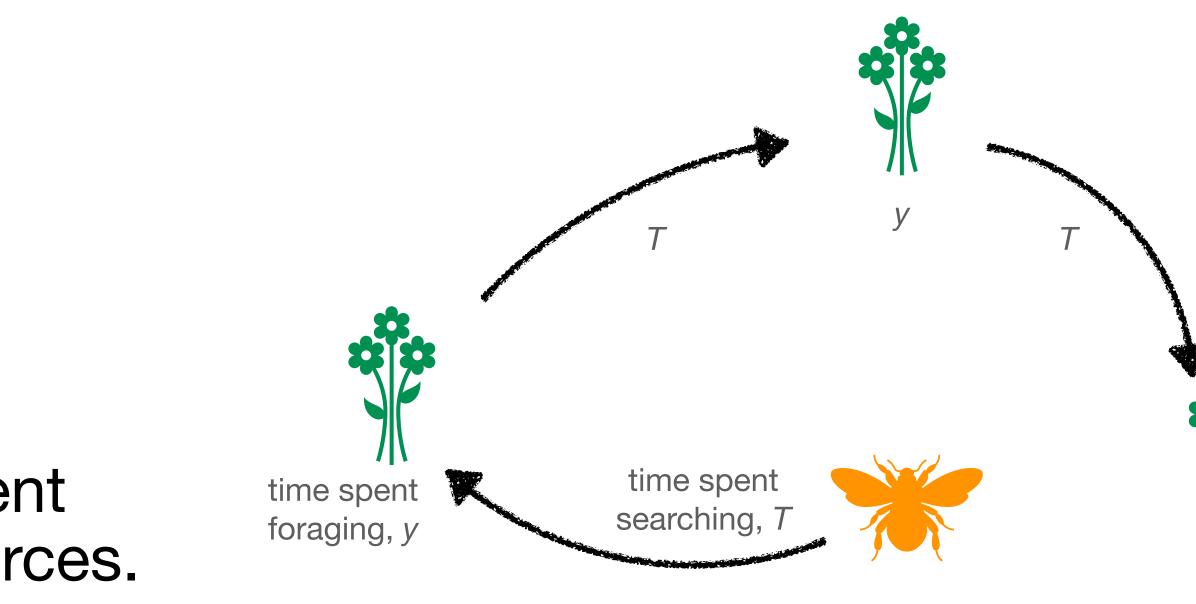


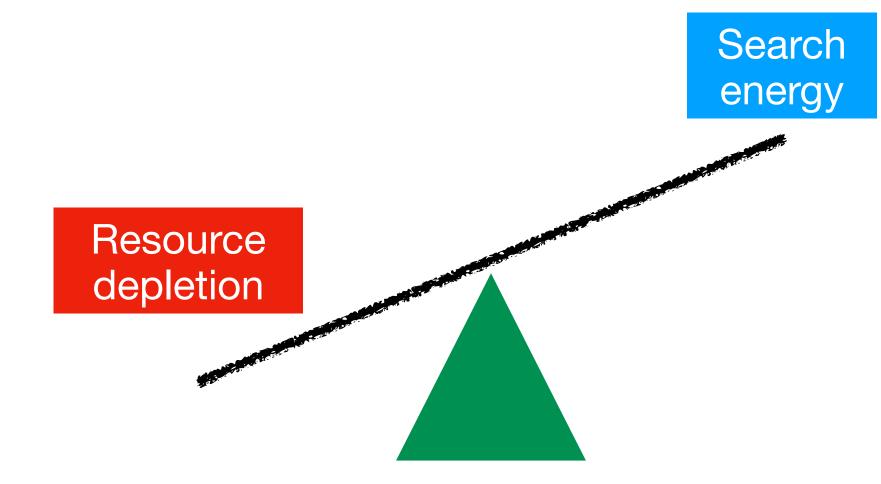
- Animal forages on multiple equivalent patches with finite amount of resources.
- How much time y should it spent foraging on a single patch when searching is costly?





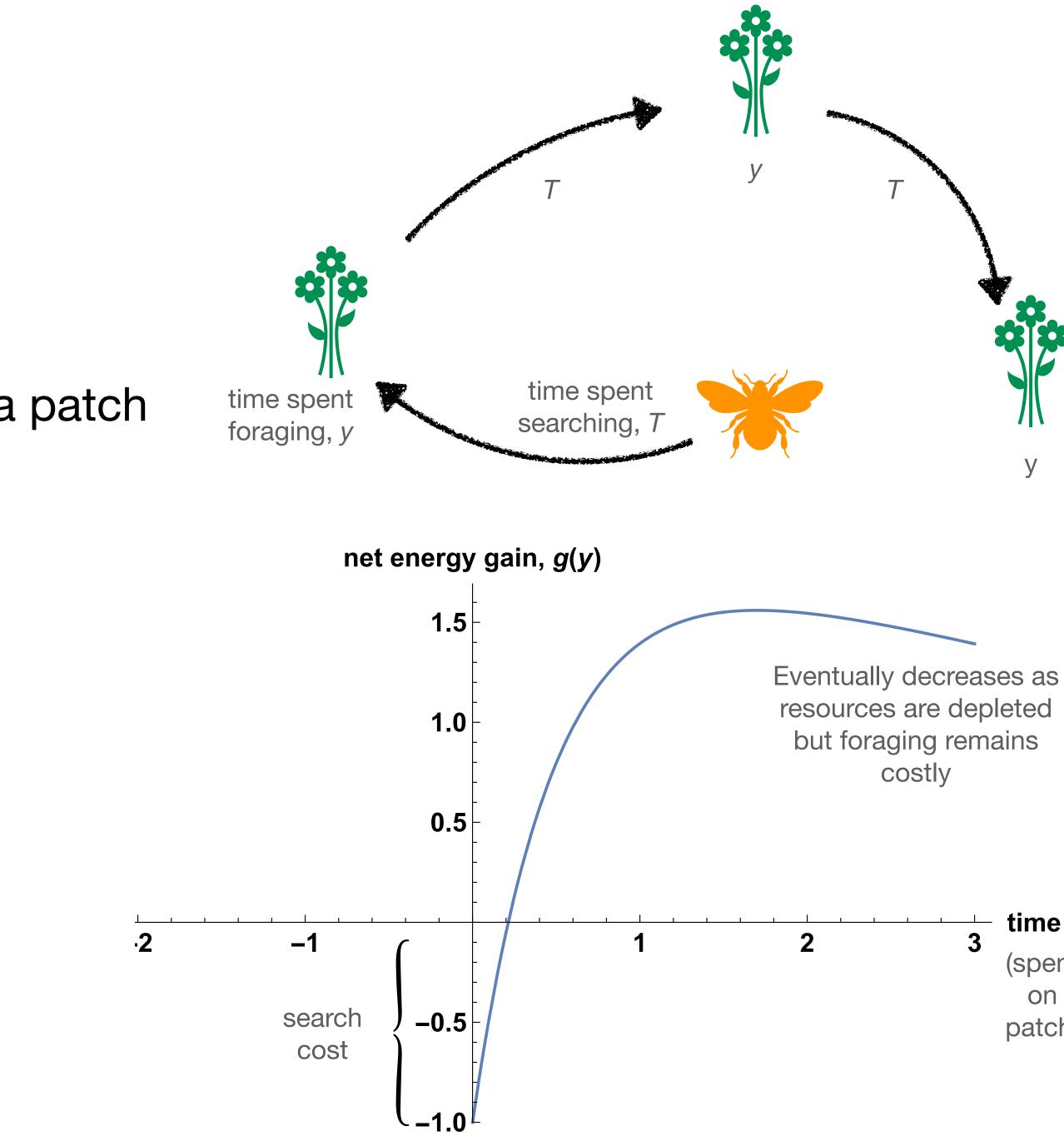
- Animal forages on multiple equivalent patches with finite amount of resources.
- How much time y should it spent foraging on a single patch when searching is costly?
- If it stays too long, resources get depleted; too short and it does not regain energy lost from search.



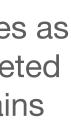




• g(y) : **net** energy gain from staying y in a patch

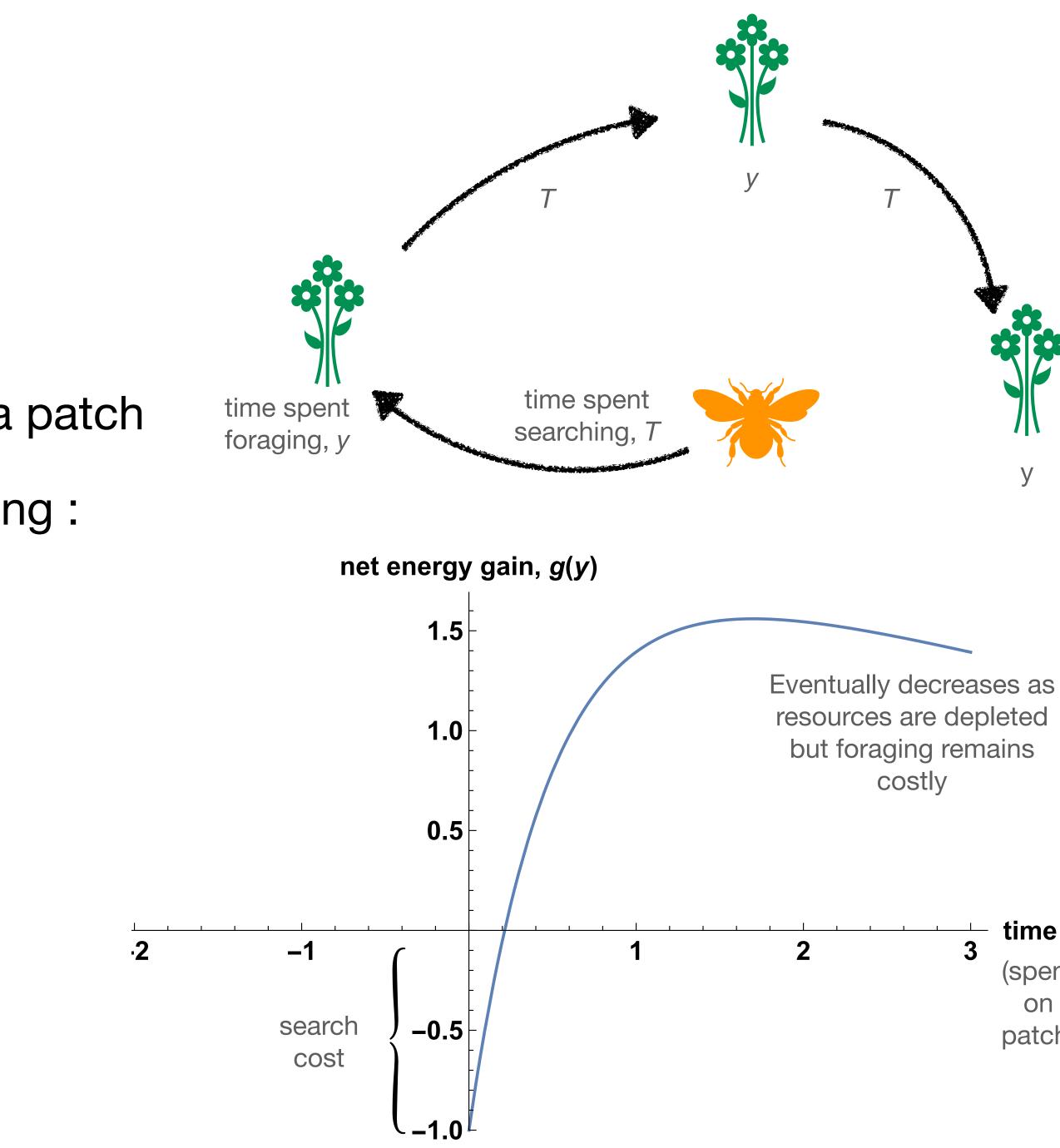




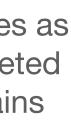




- g(y) : **net** energy gain from staying y in a patch
- Rate of energy gain from search + foraging :



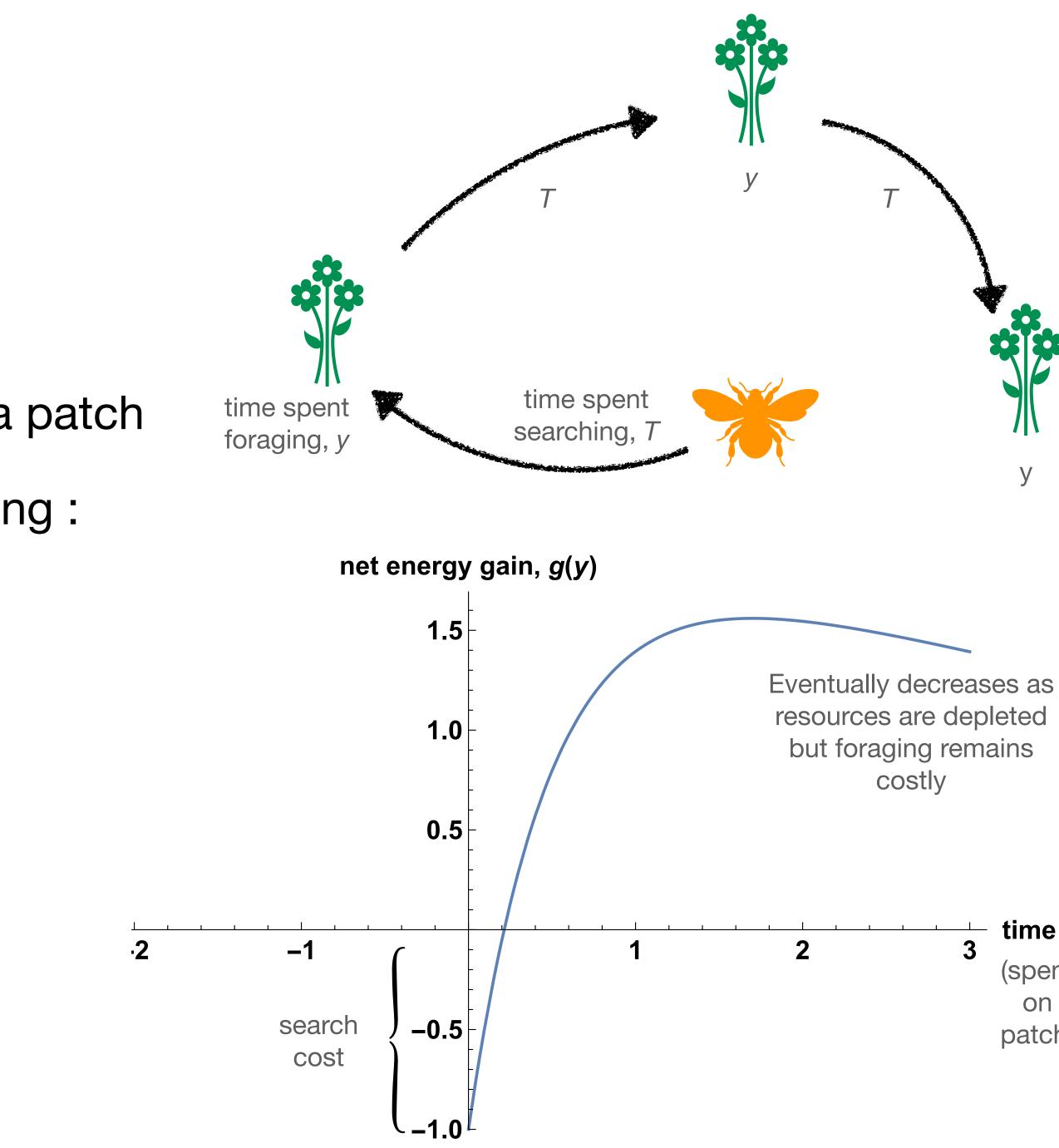




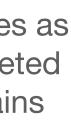


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$$R(y) = \frac{g(y)}{y+T}$$





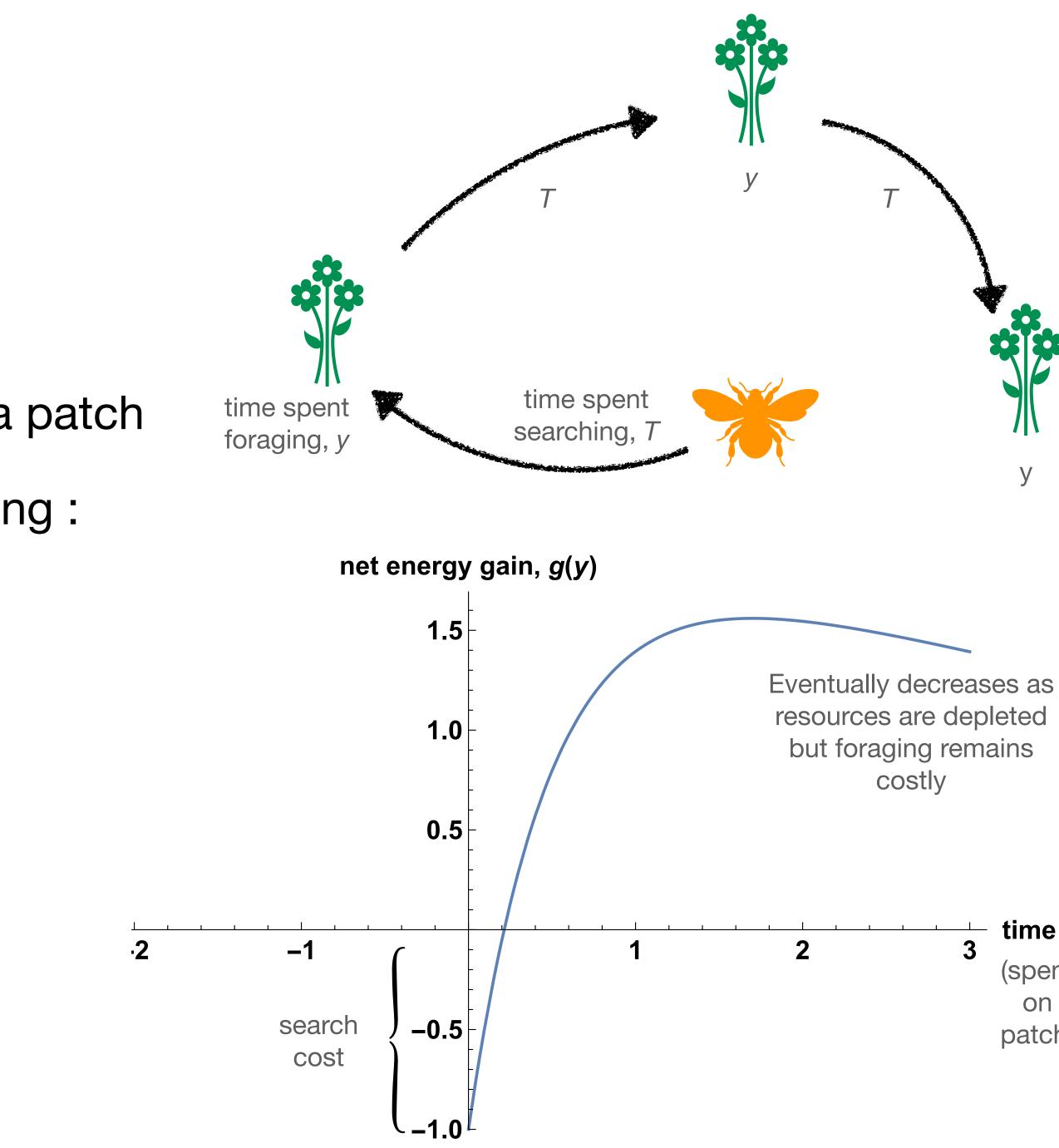




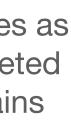
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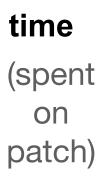
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• Fitness : $w(y, x) \propto R(y)$







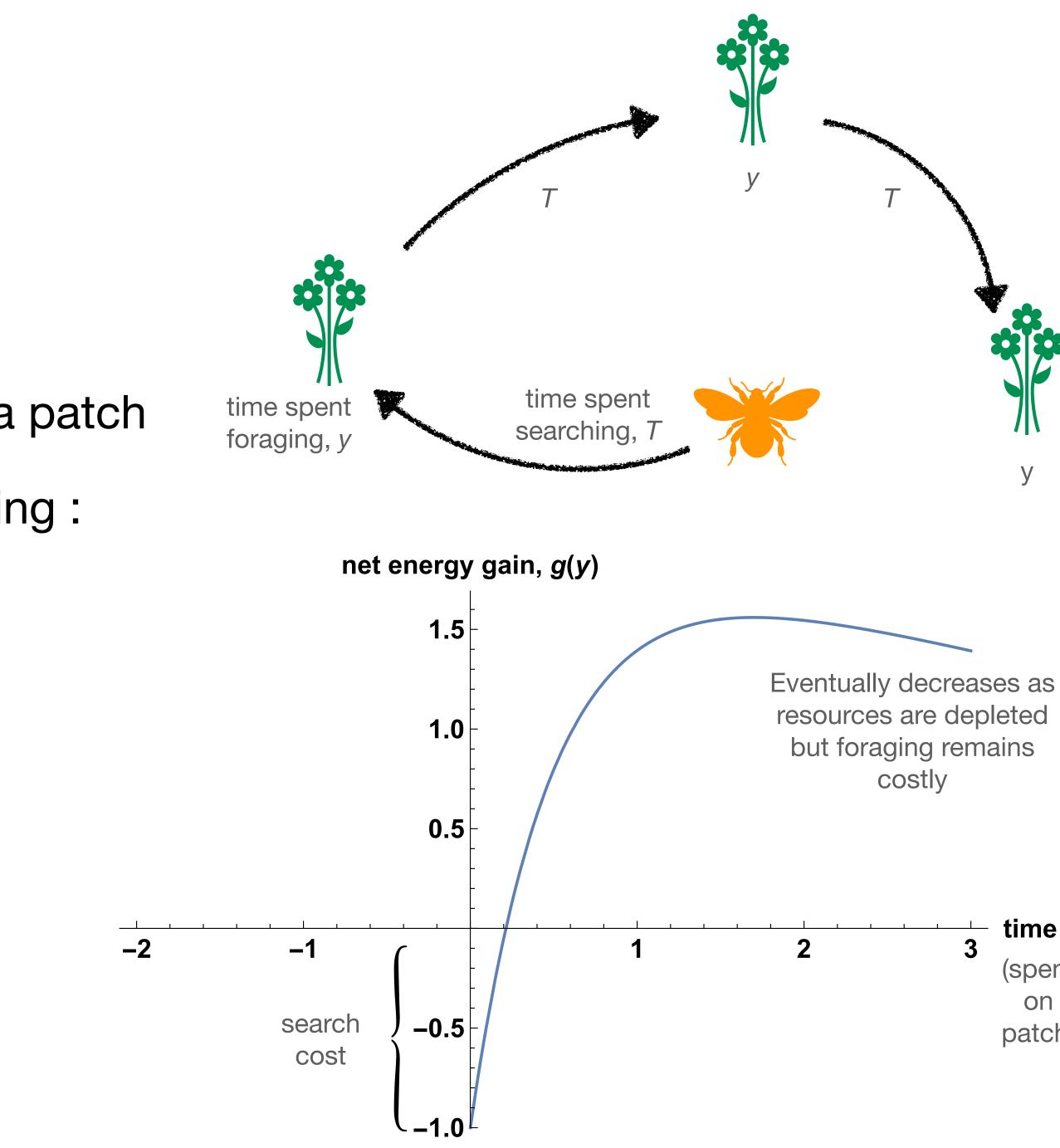


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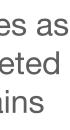
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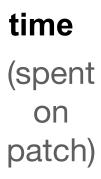
- Fitness : $w(y, x) \propto R(y)$
- Selection gradient :

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





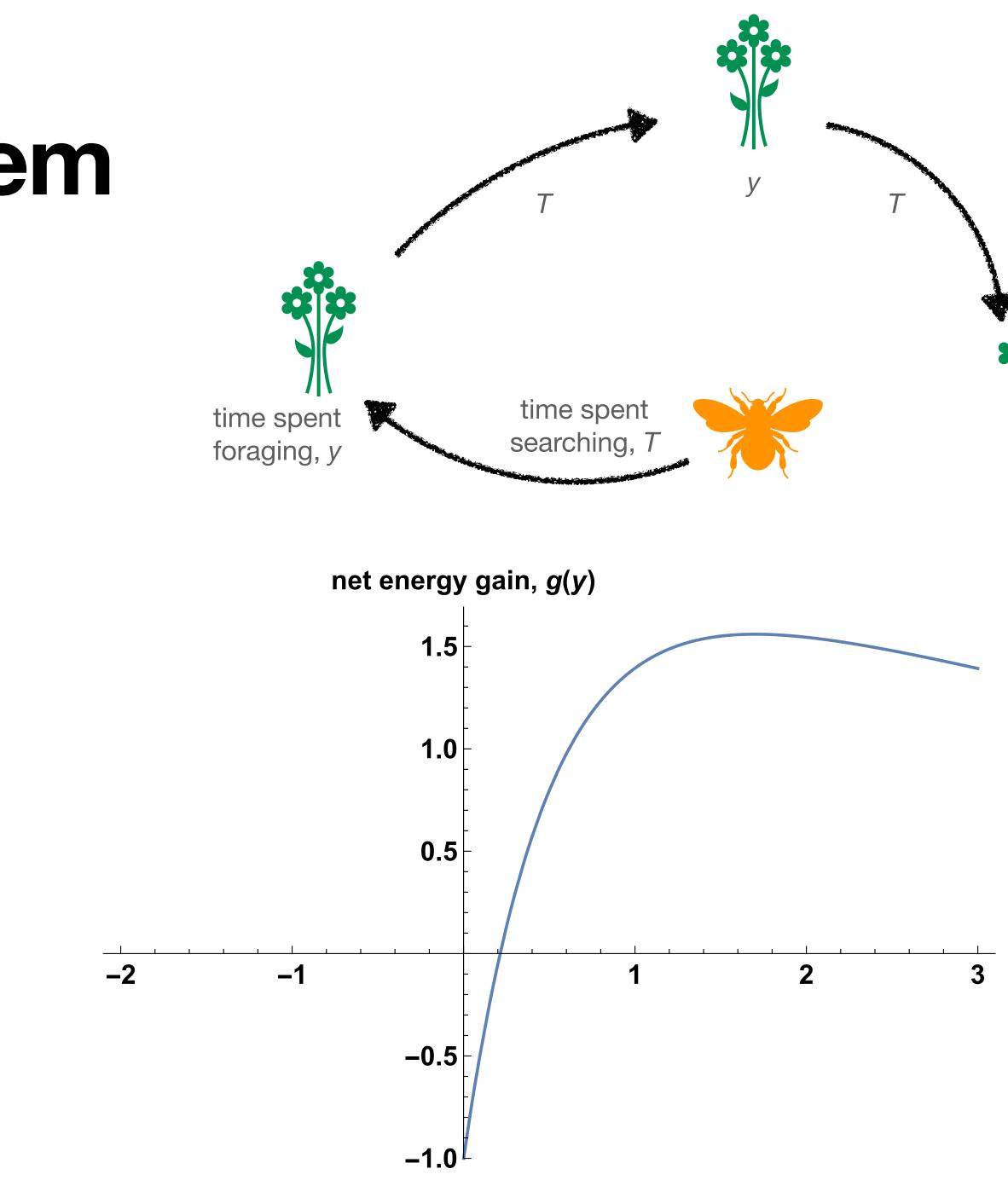




Marginal value theorem

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

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



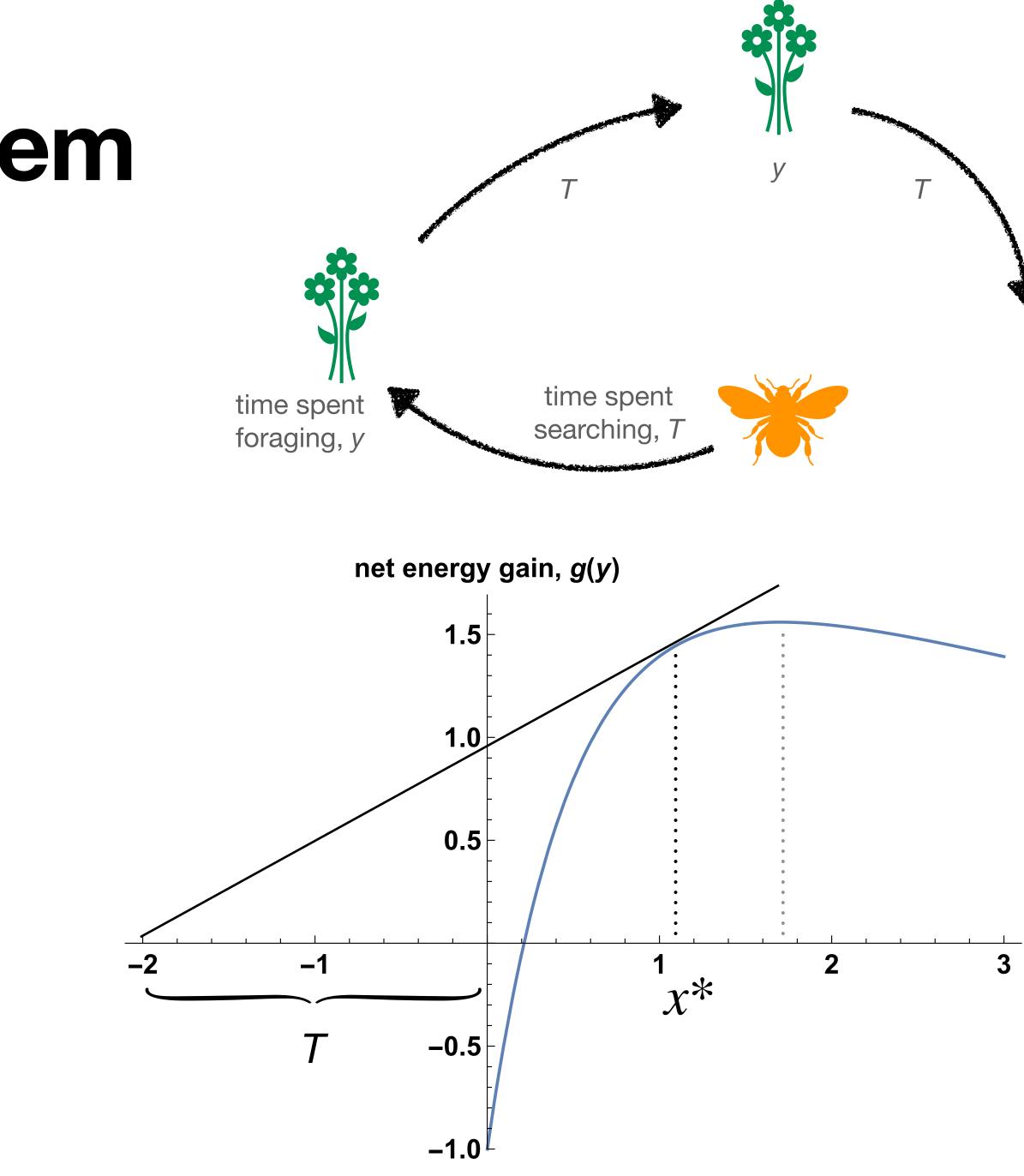




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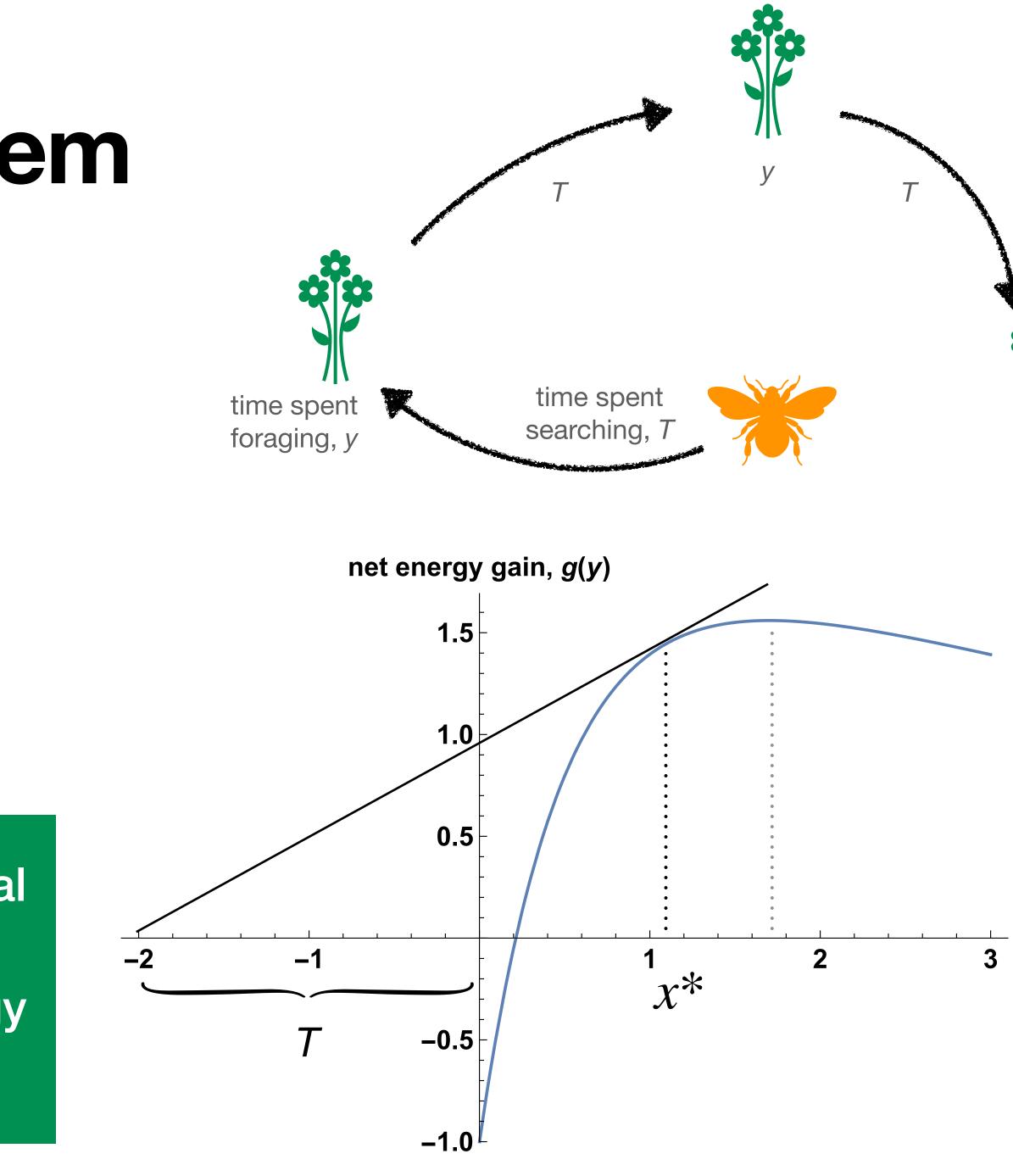


Marginal value theorem

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

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







When selection favours risky foraging?

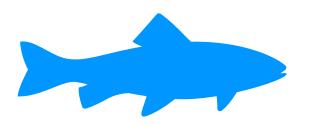
When selection favours risky foraging? Variation in relationship with uncertainty





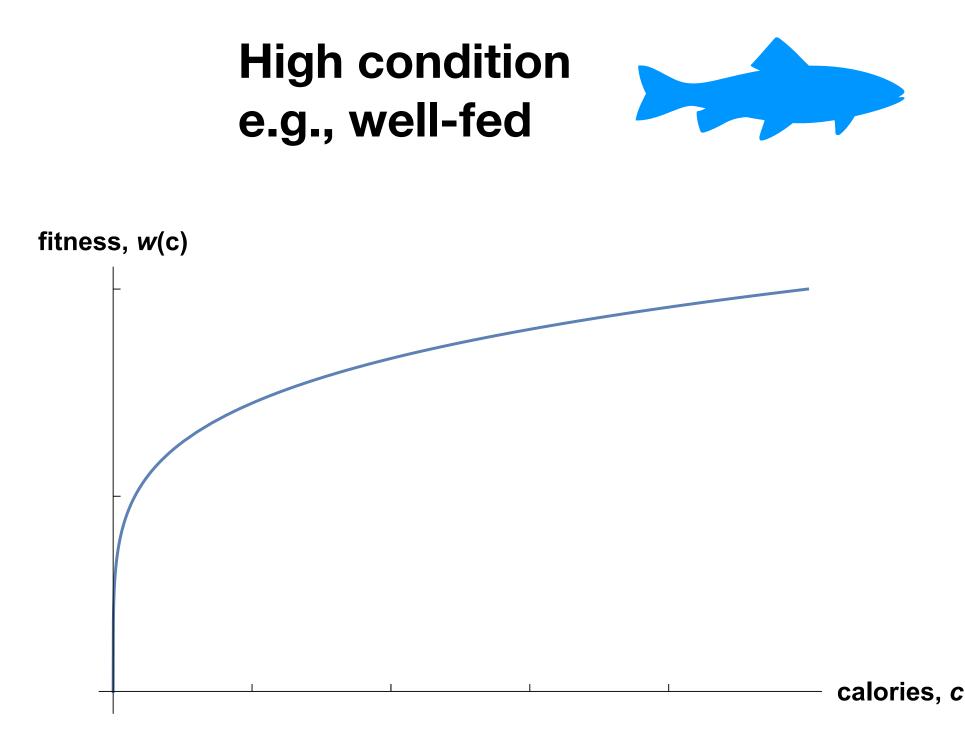


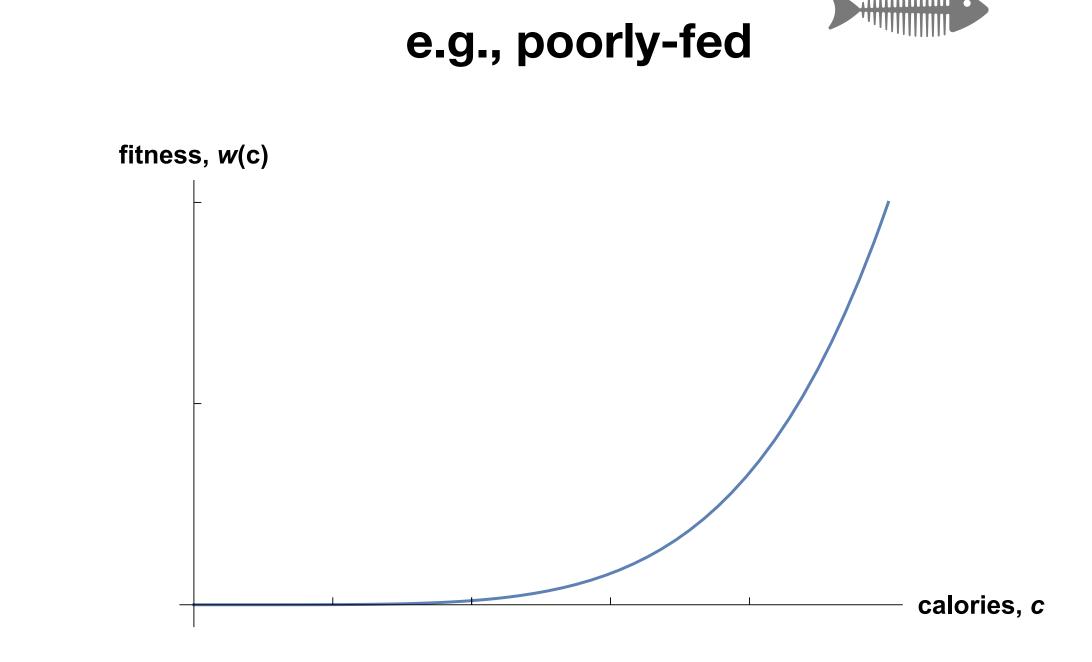
High condition e.g., well-fed

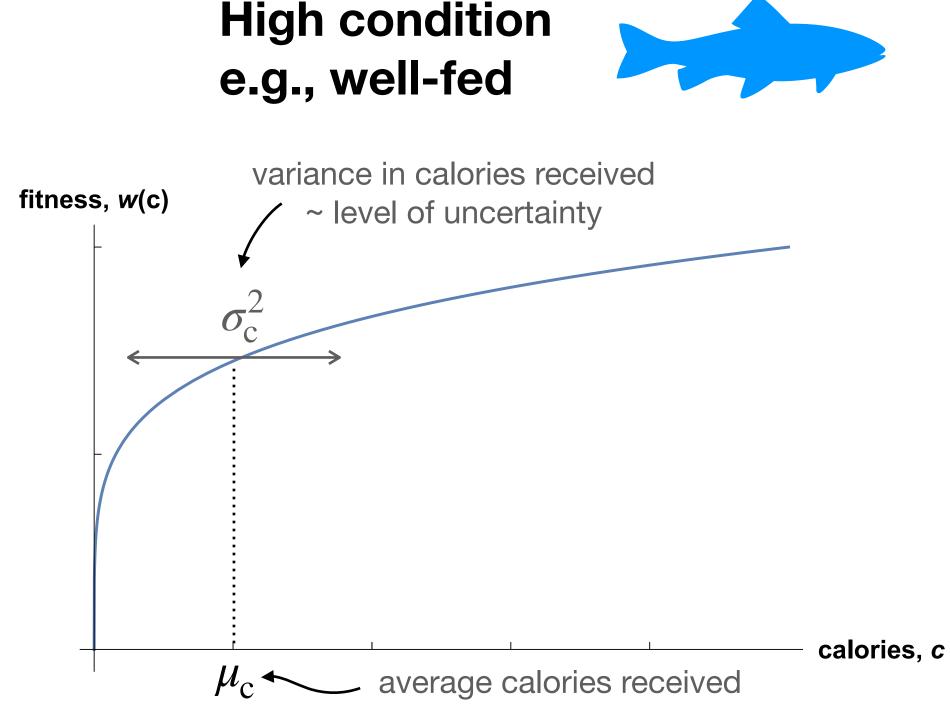


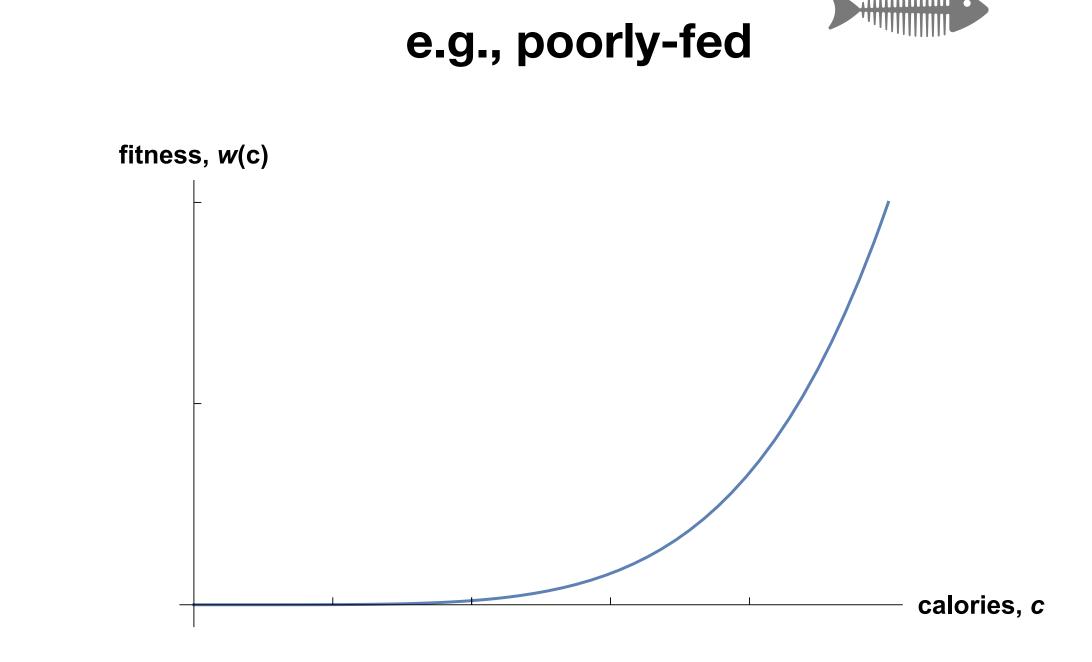
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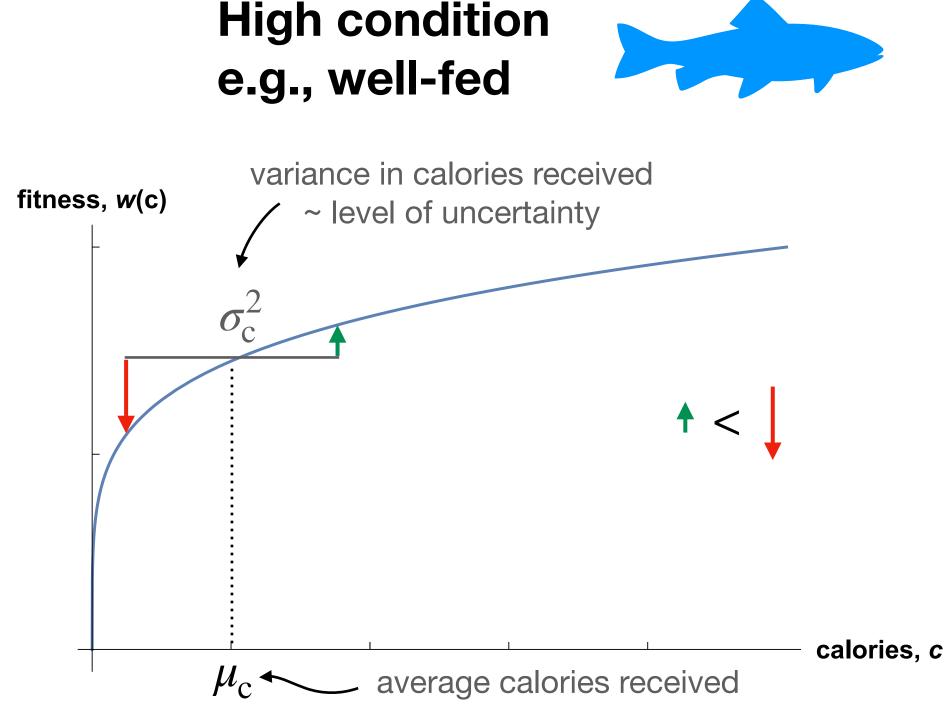


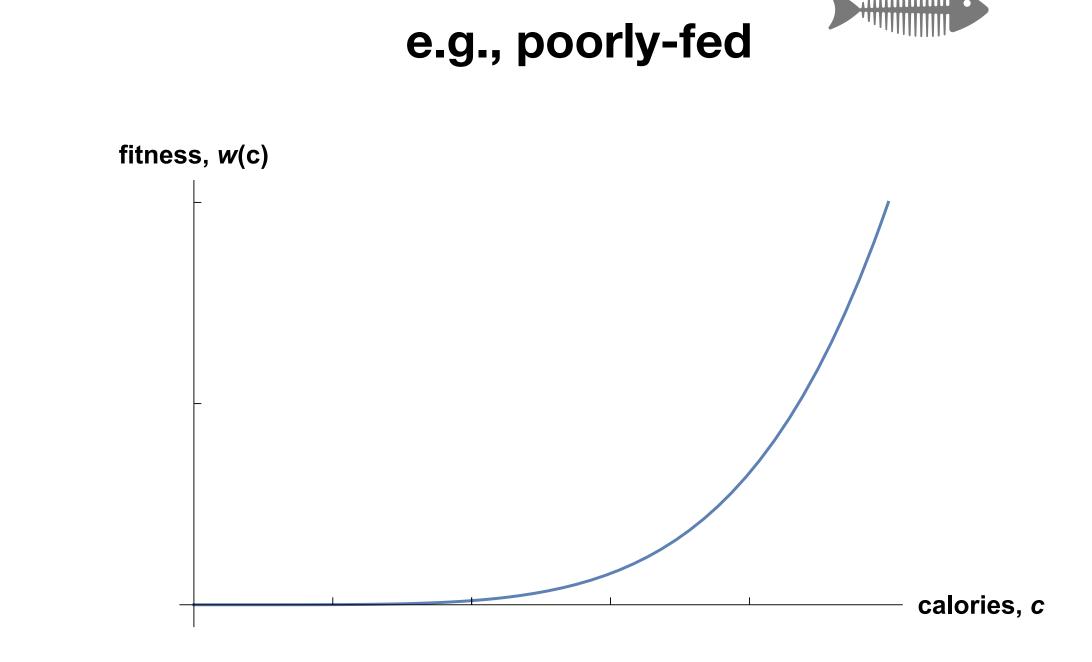


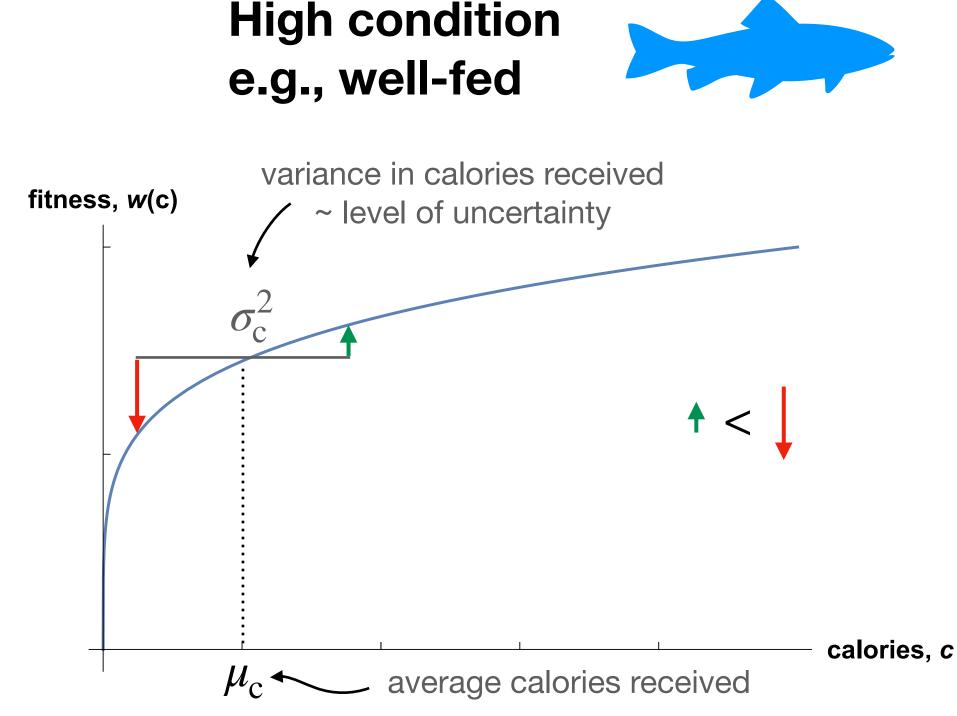




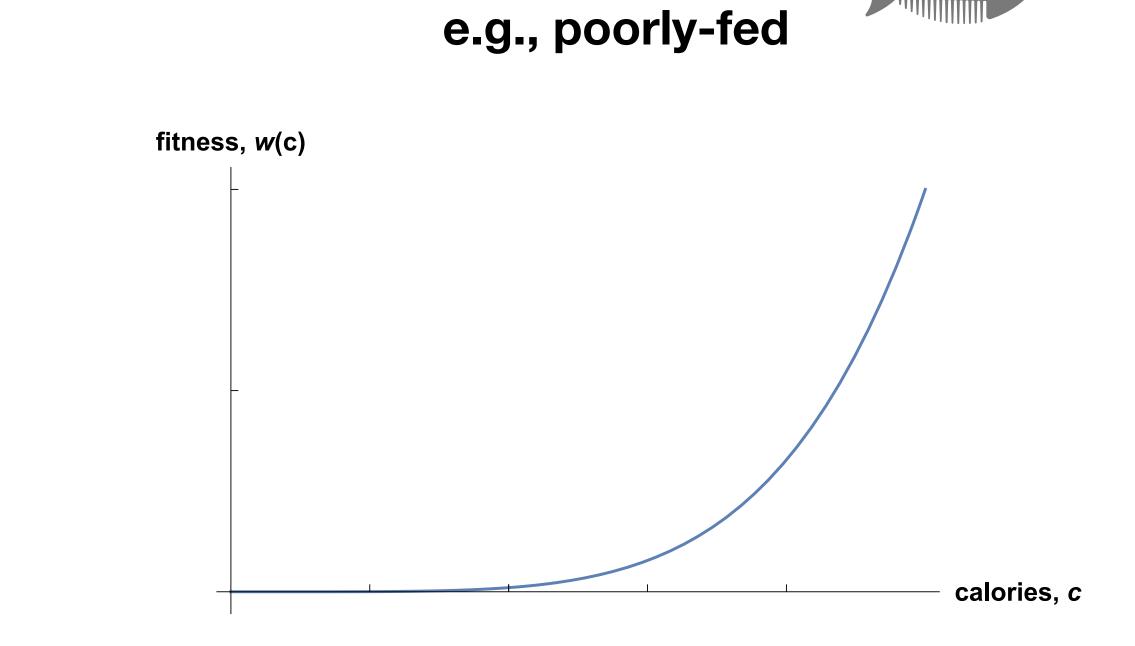


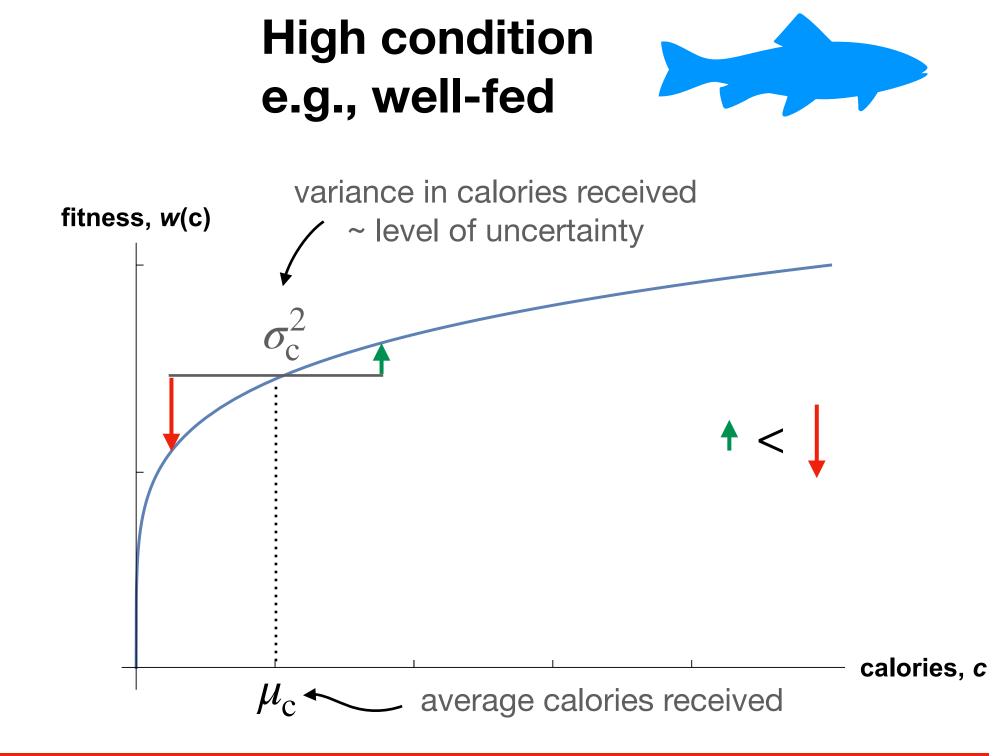




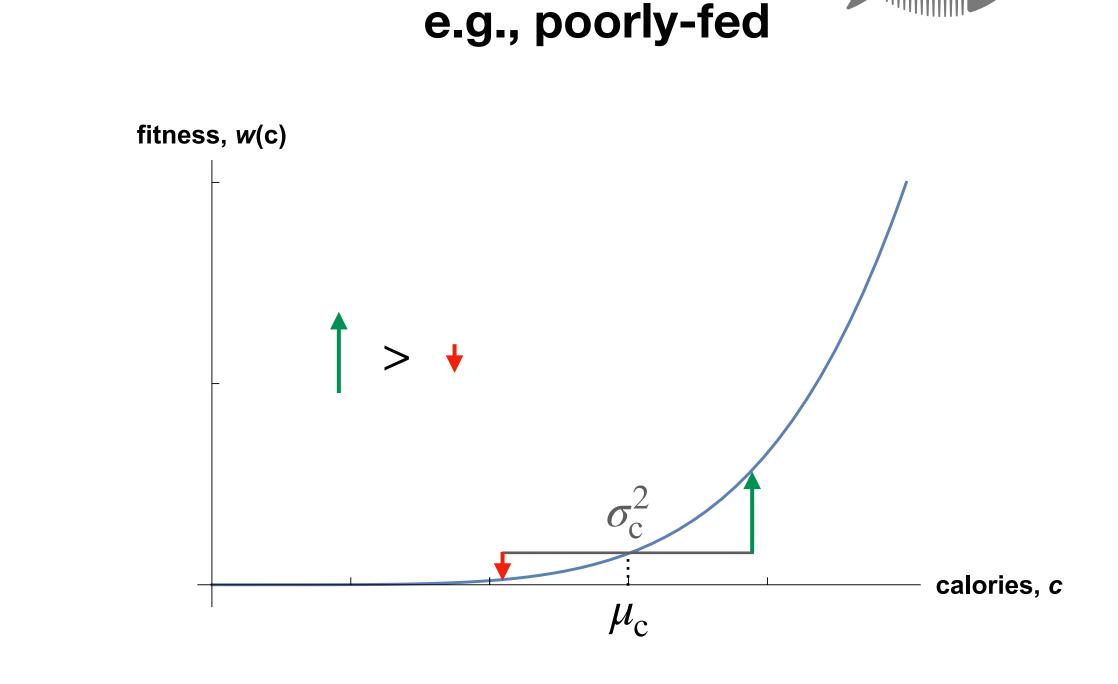


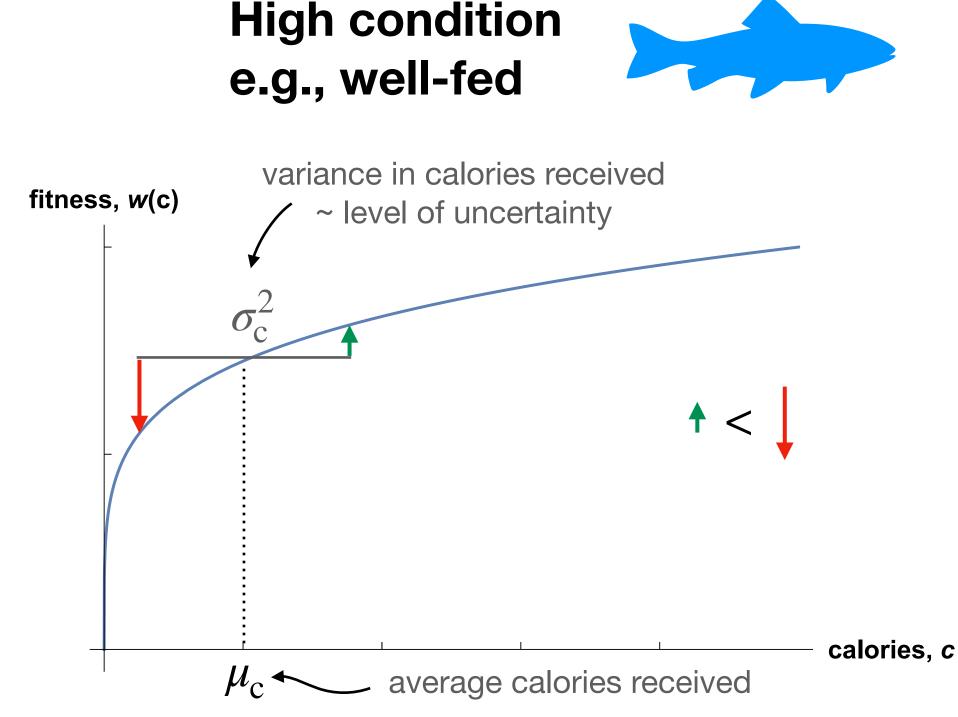
Risk not worth taking: fitness cost of bad times outweighs fitness benefits of good times



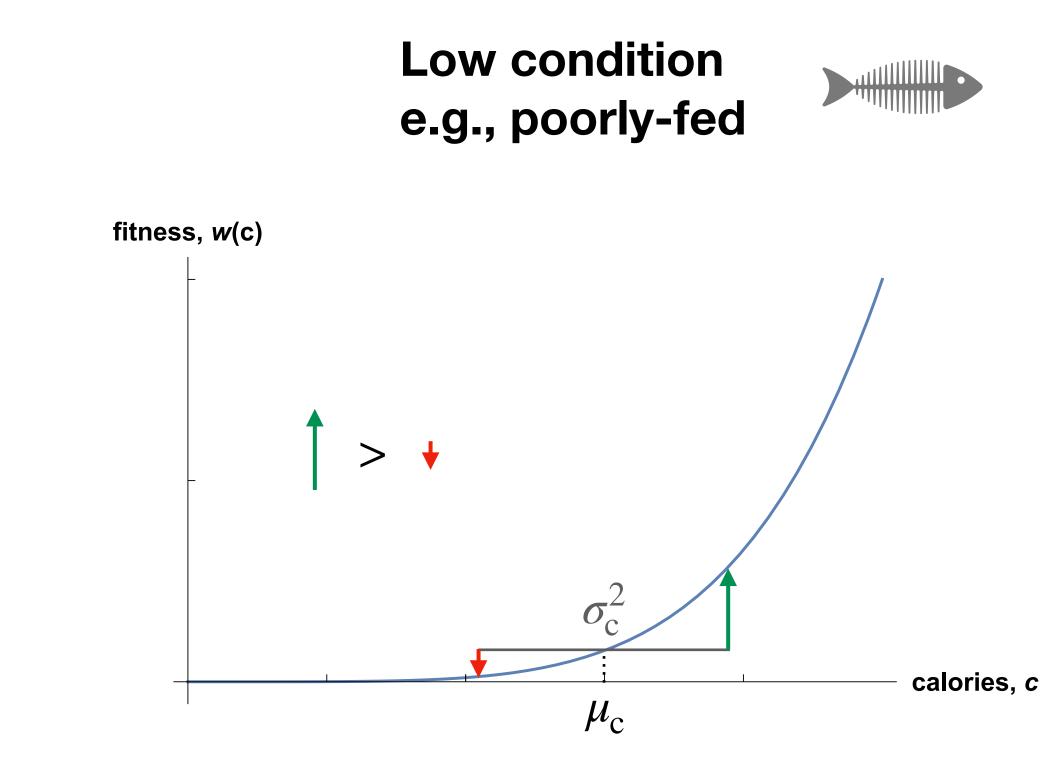


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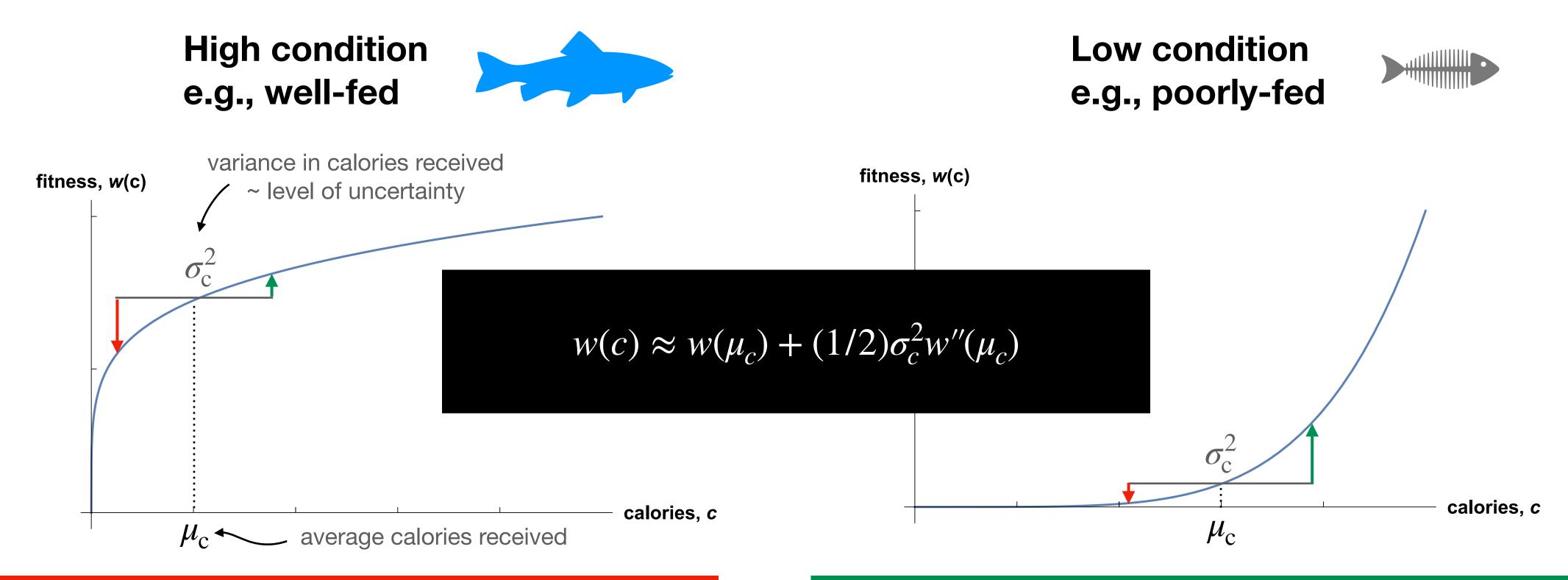


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Risk worth taking: fitness benefits of good times outweigh fitness cost of bad times





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The exploitation of renewable resources

• Biotic resource with density *n*,

$$\frac{dn}{dt} = r\left(1 - \frac{n}{K}\right)n - n_{\rm c}h(x)n$$

logistic growth

resource density, *n* 1000 800 foraging function 600 400 200 ⊢ time 10 2 8 6 4 harvesting by population of n_c consumers with foraging effort *x*

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

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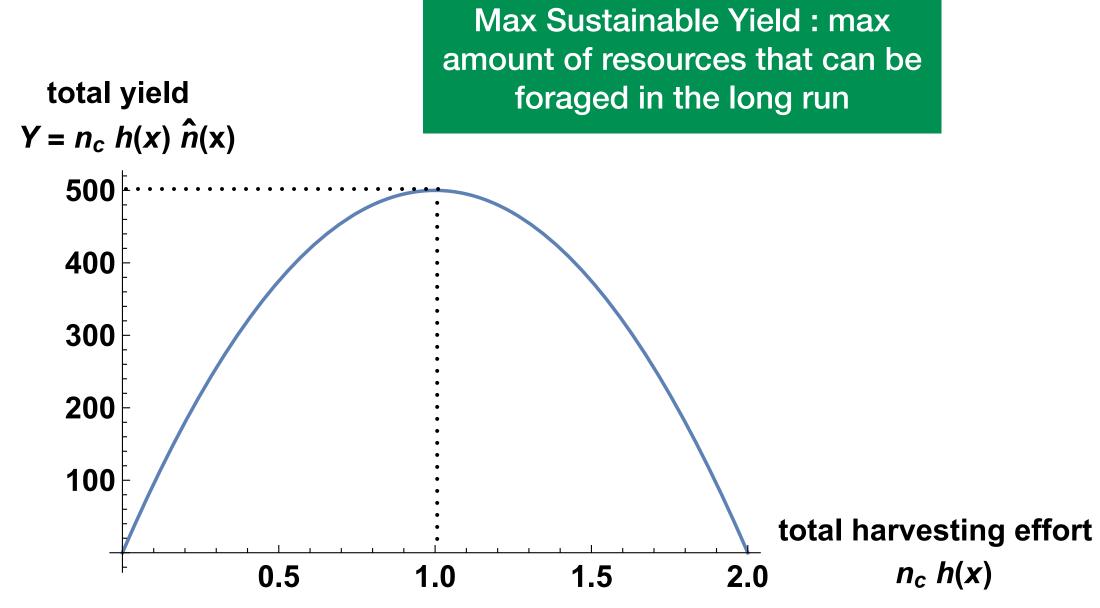
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logistic growth

resource density, *n* 1000 800 foraging function 600 400 200 time 10 8 2 6 harvesting by population of n_c consumers with total yield Max Sustainable Yield : max foraging effort *x* $Y = n_c h(x) \hat{n}(x)$ amount of resources that can be 500 foraged in the long run 400 300 200 100 total harvesting effort $n_c h(x)$ 0.5 1.0 1.5 2.0

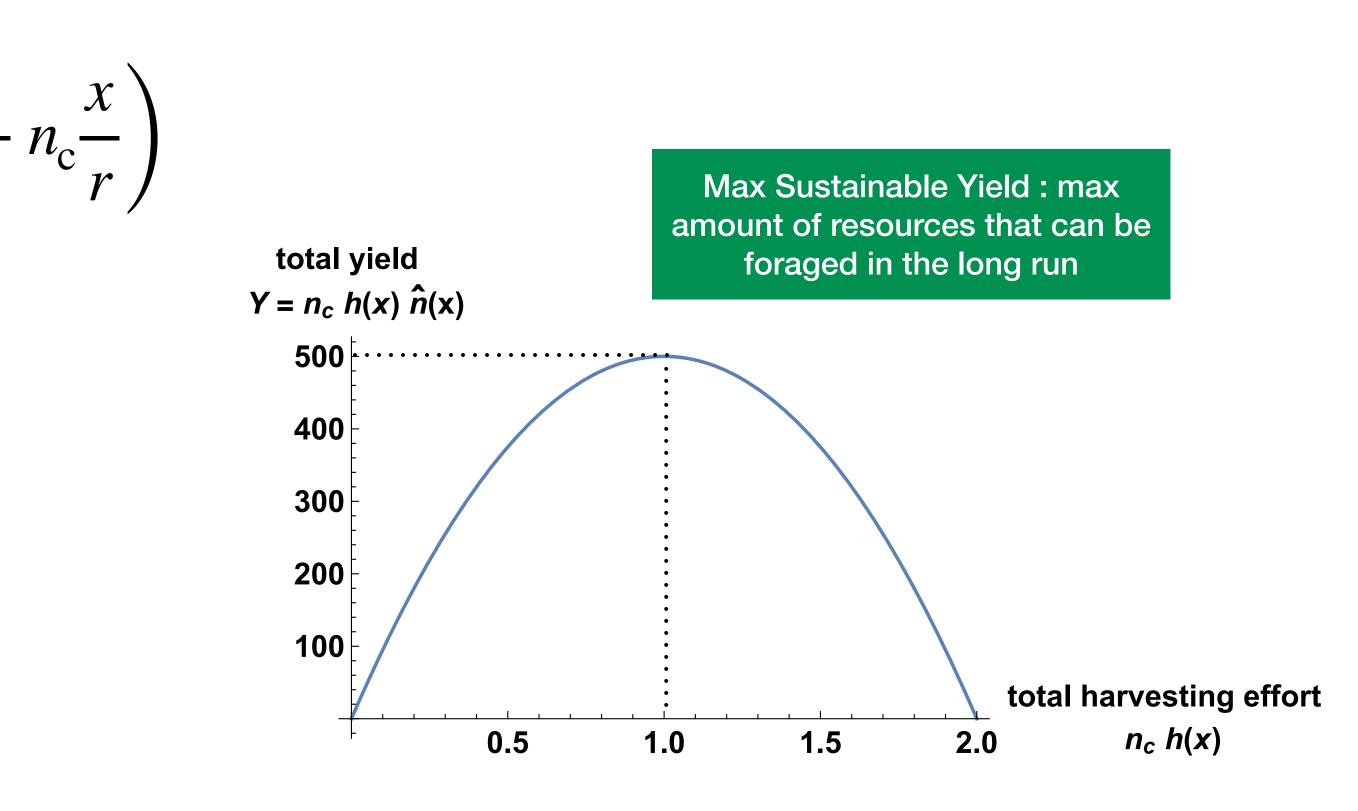
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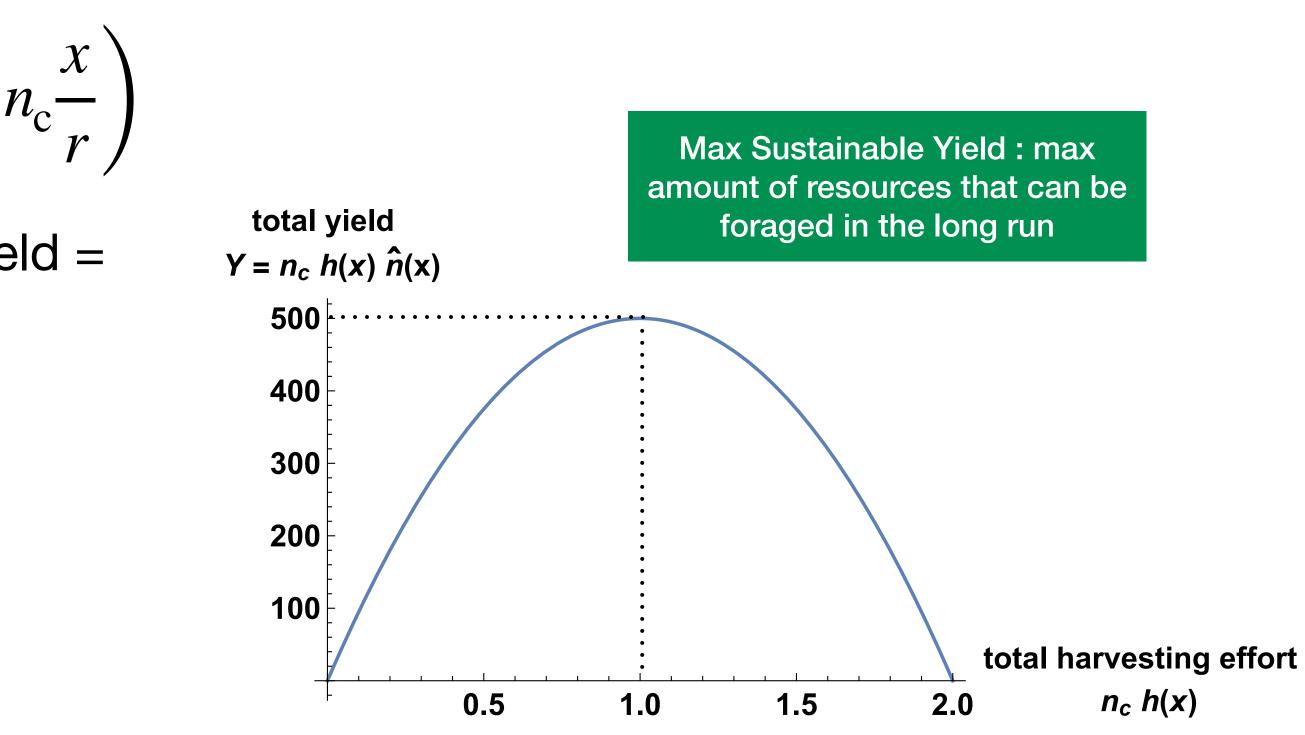




 $\int_{a}^{b(x) = x} h(x) = n_{c}h(x) \times \hat{n}(x) = n_{c}x \times K\left(1 - n_{c}\frac{x}{r}\right)$

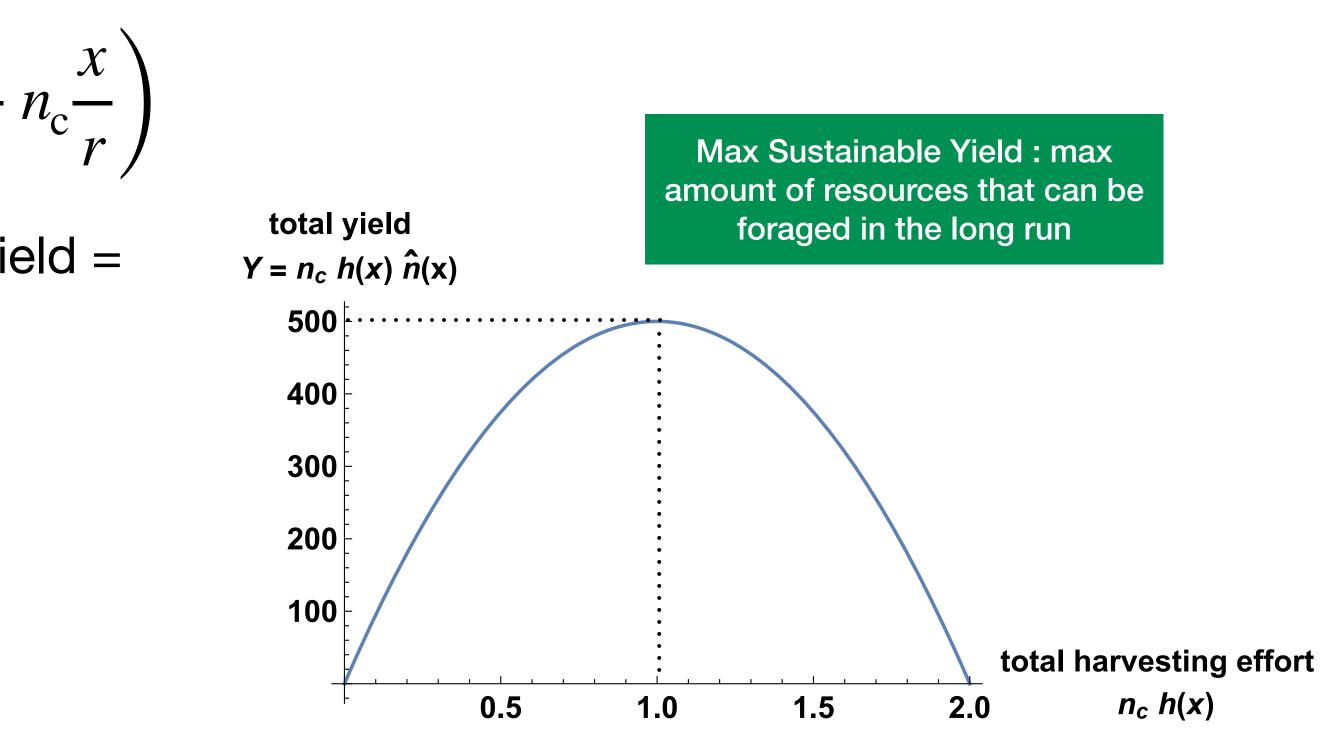


• Total yield = $n_c h(x) \times \hat{n}(x) = n_c x \times K \left(1 - n_c \frac{x}{r}\right)$



$$\int_{a}^{b(x) = x} h(x) = n_{c} x \times K \left(1 - n_{c} x \times K \right)$$

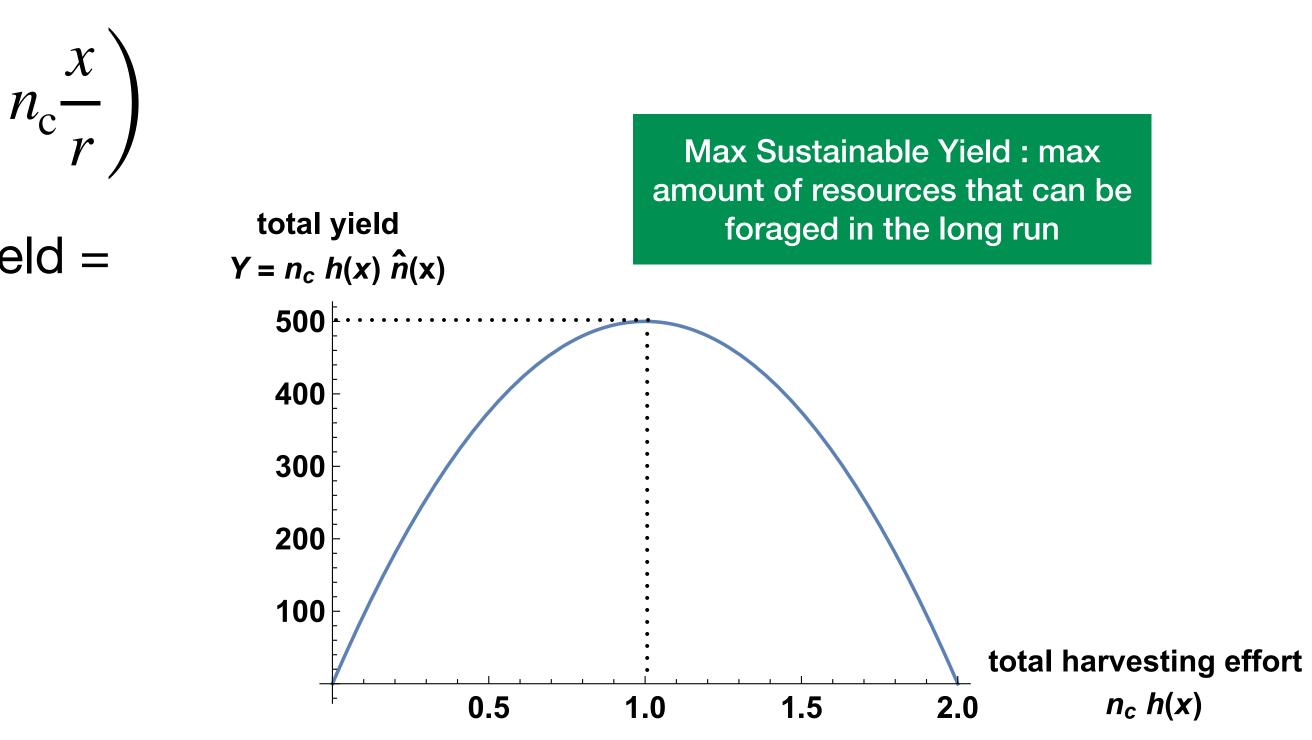
$$x_{\rm MSY} = \frac{1}{n_{\rm c}} \frac{r}{2}$$



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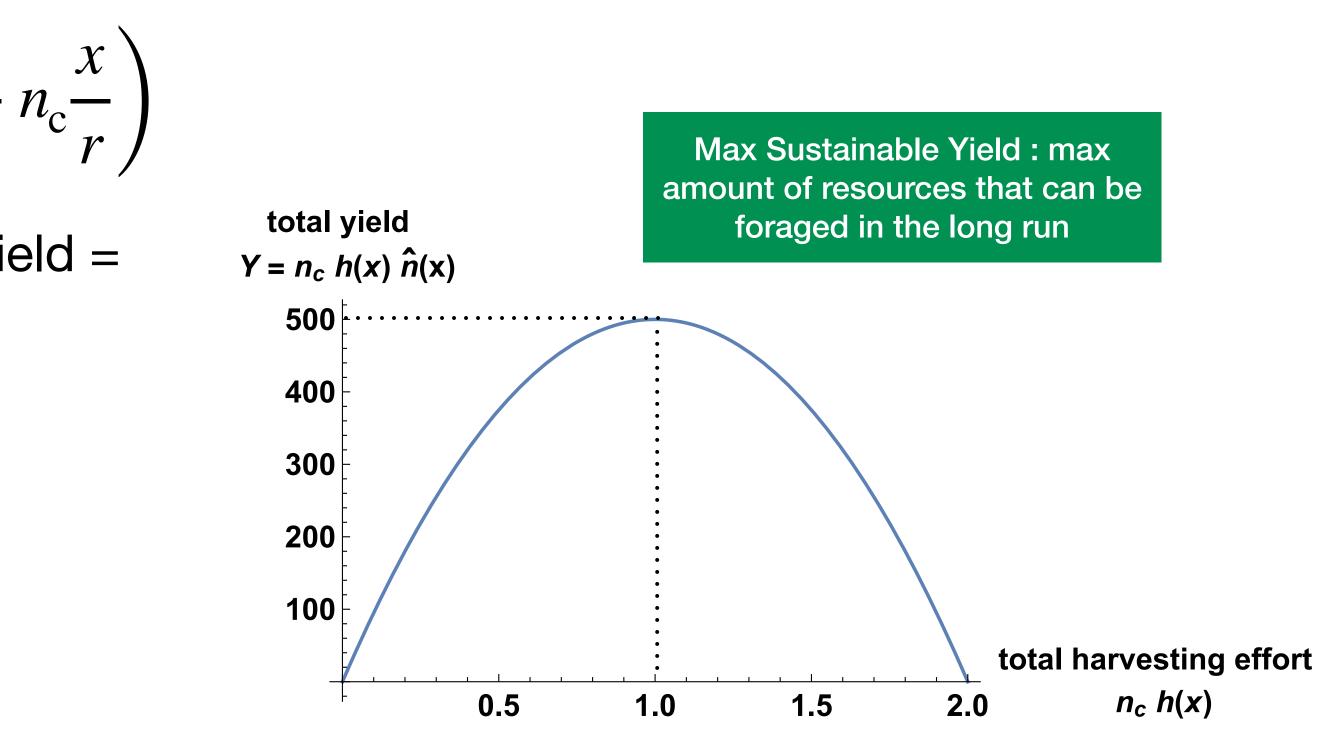
• MSY = $n_{\rm c} h(x_{\rm MSY}) \times \hat{n}(x_{\rm MSY}) = \frac{Kr}{4}$



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• MSY = $n_{\text{c}}h(x_{\text{MSY}}) \times \hat{n}(x_{\text{MSY}}) = \frac{Kr}{4}$
• Resource density = $\hat{n}(x_{\text{MSY}}) = \frac{K}{2}$



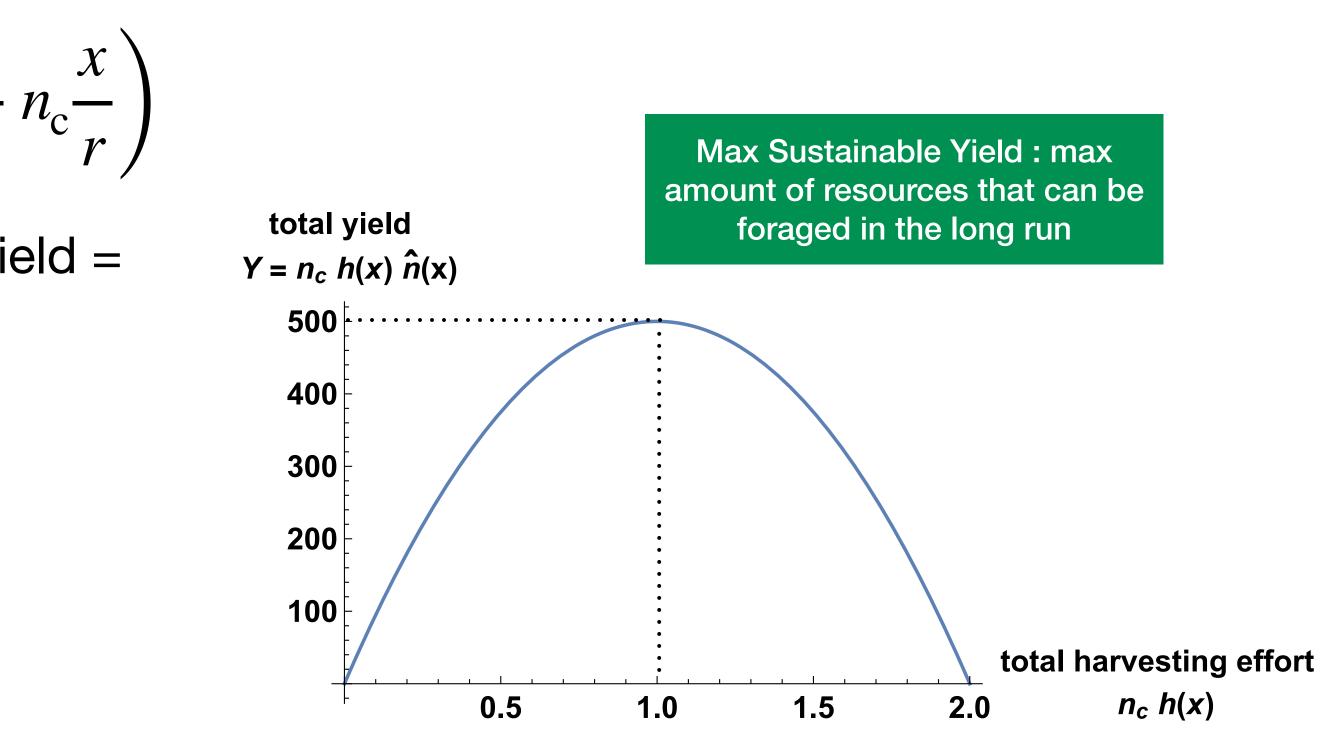
• Total yield =
$$n_c h(x) \times \hat{n}(x) = n_c x \times K \left(1 - \frac{1}{2}\right)$$

• x_{MSY} : Foraging effort that maximises total yield =

$$x_{\text{MSY}} = \frac{1}{n_{\text{c}}} \frac{r}{2}$$

• MSY = $n_{\text{c}}h(x_{\text{MSY}}) \times \hat{n}(x_{\text{MSY}}) = \frac{Kr}{4}$
• Resource density = $\hat{n}(x_{\text{MSY}}) = \frac{K}{2}$

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



 Well-mixed population where individuals all exploit the same resource and compete with one another.

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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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- Optimal strategy x^* such that $\hat{n}(x^*) = c'(x^*)$

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$$x^* = x_{MSY} \frac{2Kn_c}{Kn_c + c_0 r}$$
 $h(x) = x$
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When cost is large, $c_0 \ge \frac{Kn_c}{1}$ then $x^* \le x_{MSY}$. Otherwise, $x^* > x_{MSY}$. When $c_0 = 0$, evolution leads to resource extinction.

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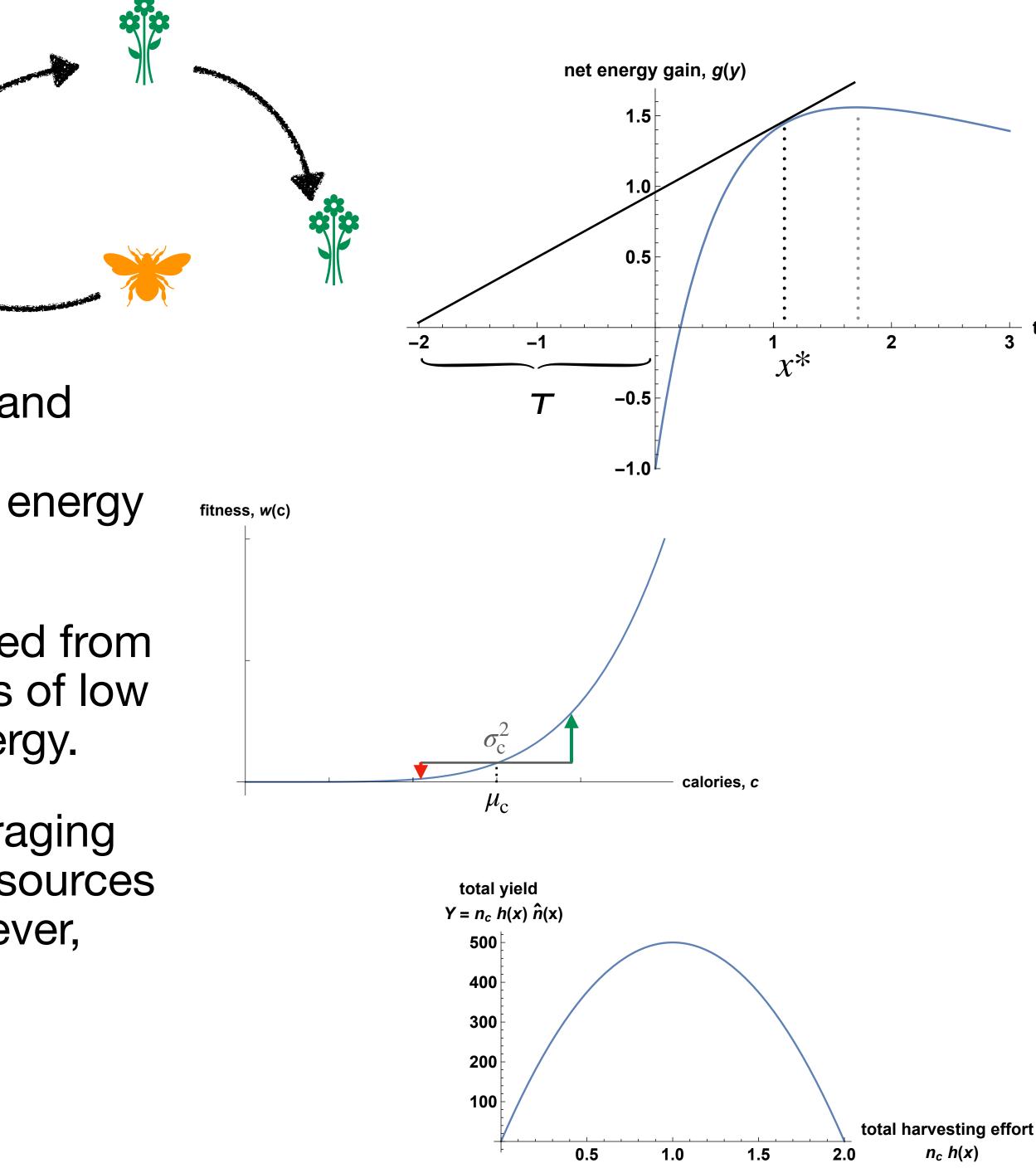
Due to competition, evolution typically leads to overexploitation and lower yield than if individuals were coordinated.

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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 overconsumption.





time