*2009年10月6日*

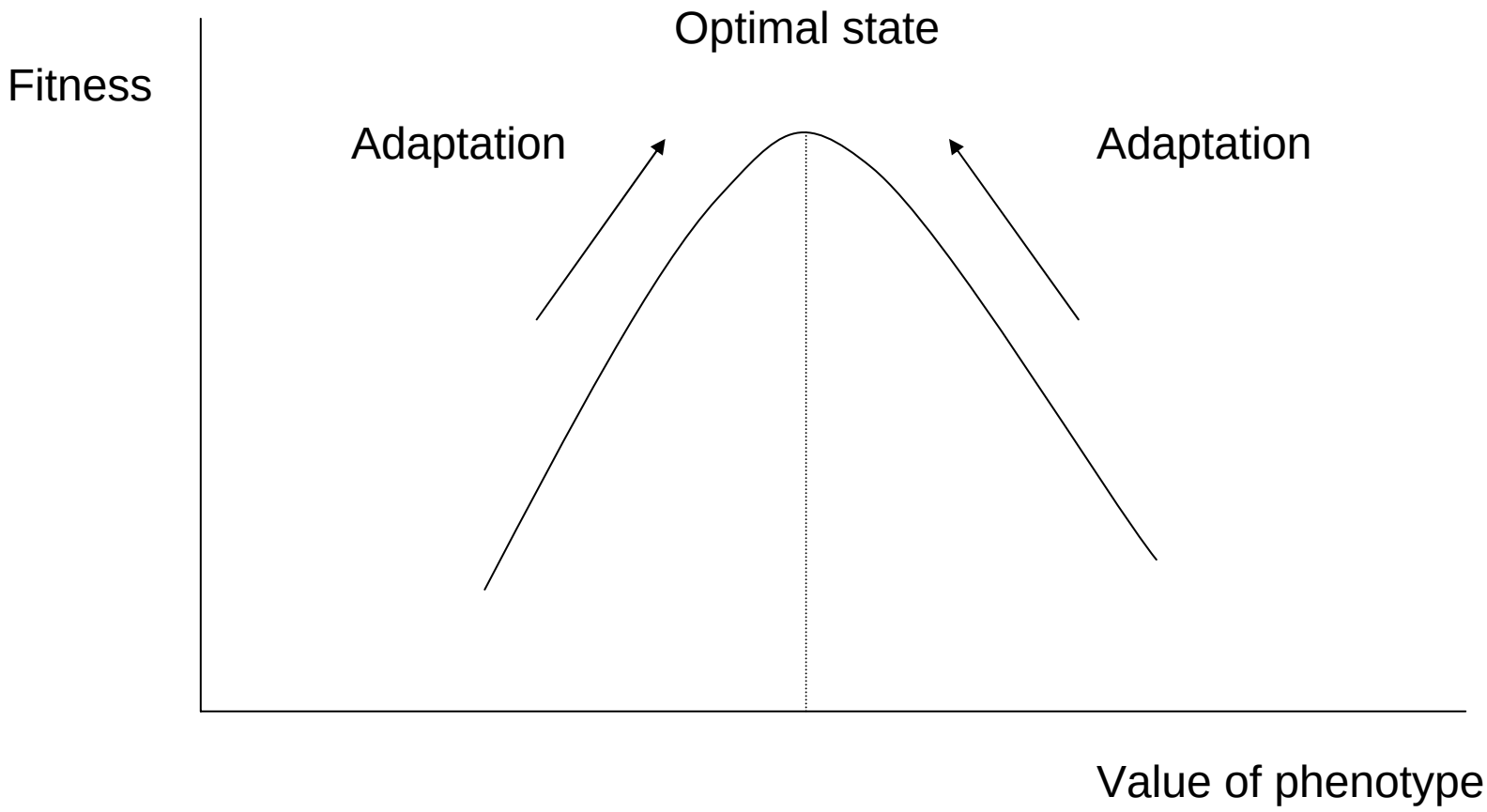
# 生態学Ⅰ　第2回

# 競争方程式 competitive equation
# 最適戦略 optimal strategy

# Adaptation and fitness

- *Adaptation*: genetic changes in phenotypes of an organism to become more fitted to an environment.
- *Fitness*: the degree of how well a phenotype is fitted to an environment.
- *How can we define and quantify the fitness?*

# Graphical representation of adaptation



# Fitness 適応度

- The capability of an individual of certain genotype to reproduce.
- The number of offspring produced through life by certain genotype.

$$W = \sum_x l_x m_x$$

生涯繁殖成功度
Lifetime reproductive success

$l_x$ $x$令までの生残率（survivorship at $x$）

$m_x$ $x$令での産卵（産仔）数（fecundity at $x$）

# Early migration of modern humans

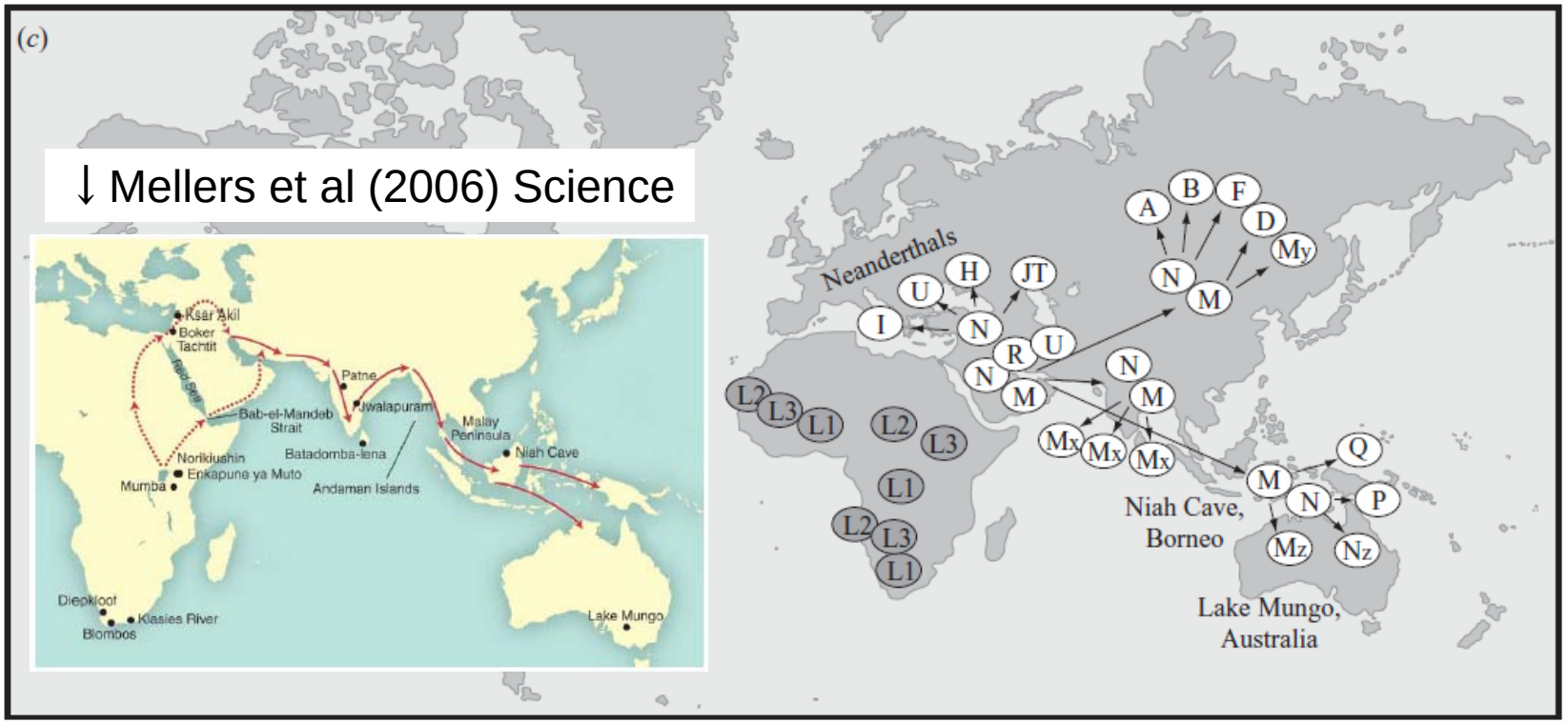



Figure 2 (*a–c*). Evolution, expansion and migration of human mtDNA types across the world: (*a*) 200–100 ka; (*b*) 80–60 ka; (*c*) 60–30 ka.

*Phil. Trans. R. Soc. Lond.* B (2004)
Foster (2004)

ネアンデルタール人が分布していないアジアでは急速に広がった
ヨーロッパへの分布拡大はより遅い・・・おそらく種間競争があった

# Question

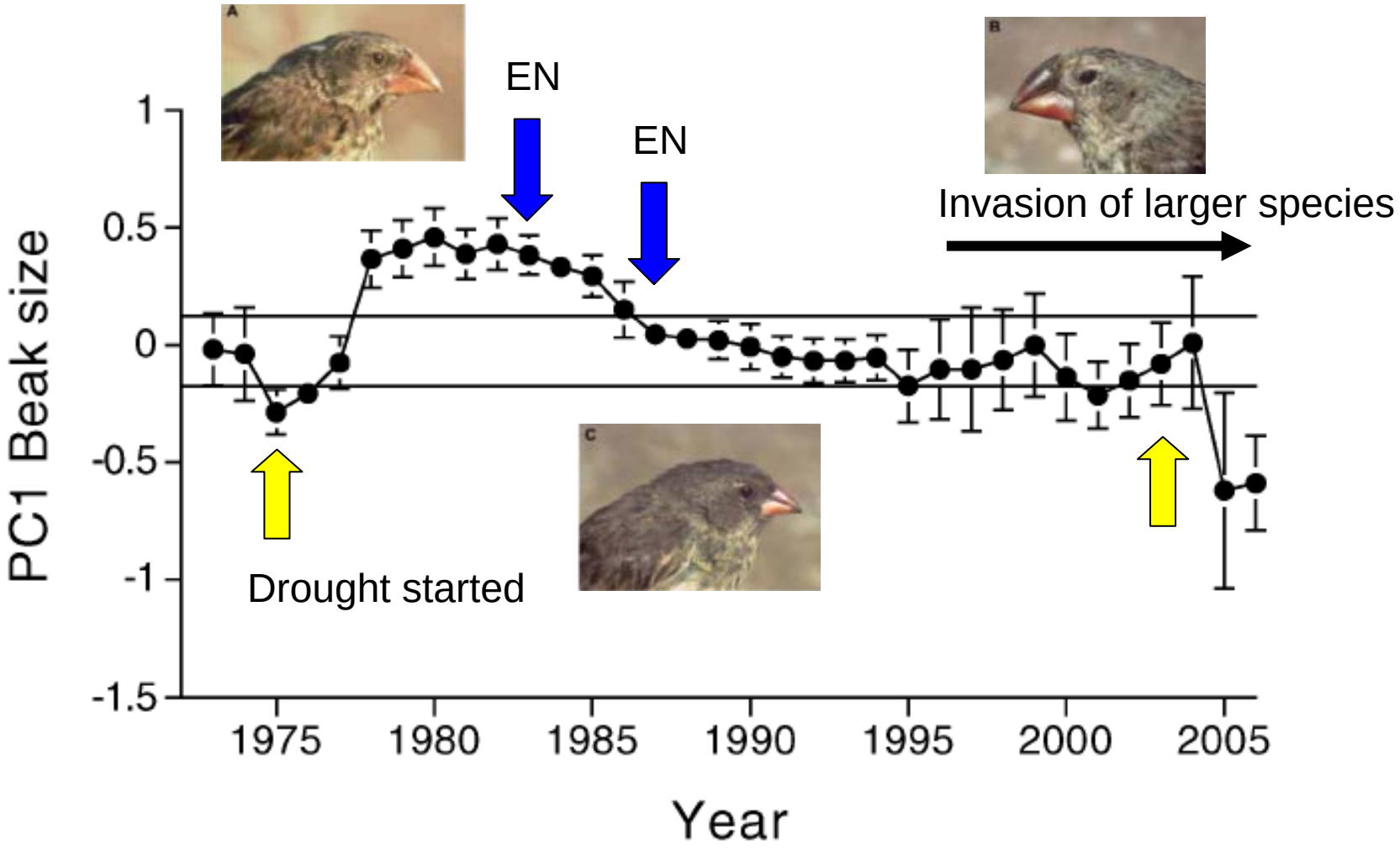
- Can we consider that the fitness of *Homo sapiens* was higher than the fitness of *Homo neanderthalensis*?
- In other words, was *Homo sapiens* more fitted to an environment than *Homo neanderthalensis* ?

# Yes

- Because *Homo sapiens* persisted longer than *H. neanderthalensis* ヒトはネアンデルタール人より後世まで残っているから(10)
- Because *Hn* became extinct 両者は同じ時期にいながらネアンデルタール人は滅びたから(4)
- Because *Hs* had a wider range より分布が広いから(8)
- Because *Hs* migrated faster ネアンデルタール人より急速に分布を広げたから(5)
- Because survivorship and fecundity increase with population size 個体数が多いと生存率や産仔数が増えるから(2)

All of these answers are wrong.

# Beak size adaptation in medium ground finches

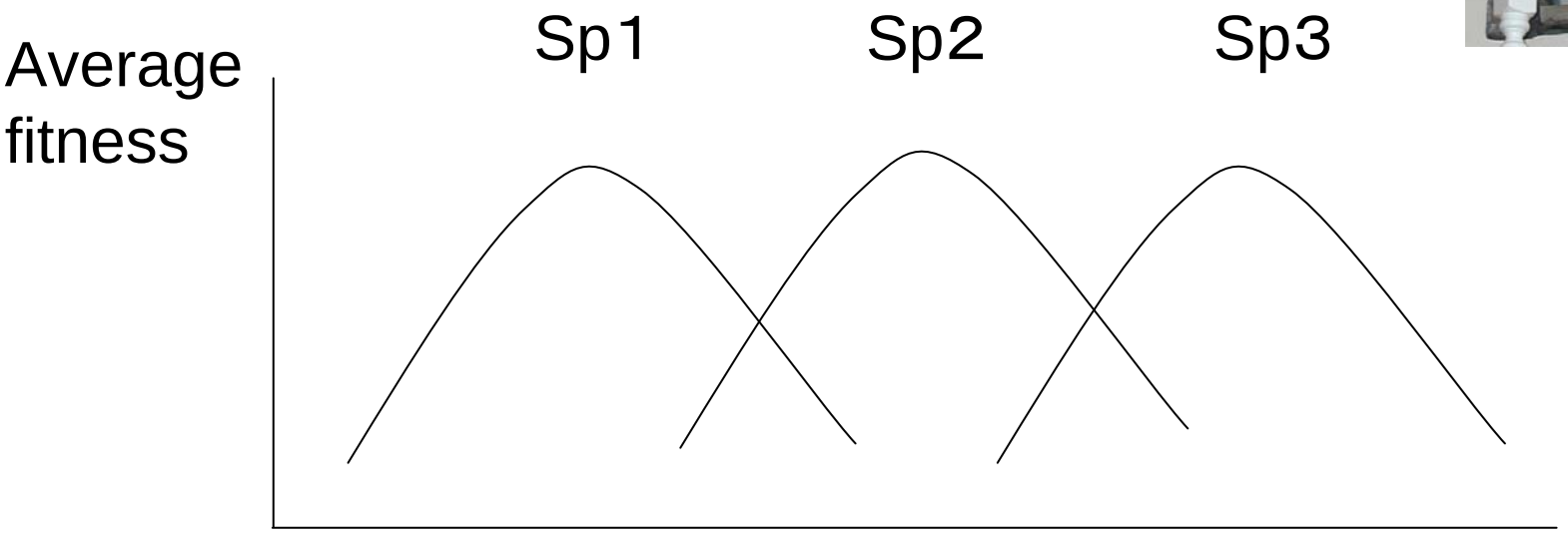



From Grant and Grant (2002)

# No

- Because *Hs* was more intelligent than *Hn*; fitness did not matter. ネアンデルタール人が滅んだのはホモサピエンスが（適応度ではなく）知恵で上回ったため(3)
  - “Intelligence” is partly heritable.
- It is impossible to compare because *Hs* and *Hn* used different resources or lived under different environments 資源・環境がちがうので両者は比較できない(8)
  - Right.
- It is impossible to compare because *Hs* and *Hn* are different species 両者は種が異なるので比較できない(3)
  - We can compare average fitness if two species compete with the same resource under the same environment.
- It is impossible to compare because difference in fecundity is unknown 産仔数が不明だから比較不能(2)

# ニッチ niche


Sp1
Sp2
Sp3
Average fitness
State of resource, not of phenotype

# Average fitness 平均適応度

$$\overline{W} = \frac{1}{n} \sum_{i=1}^{n} w_i$$

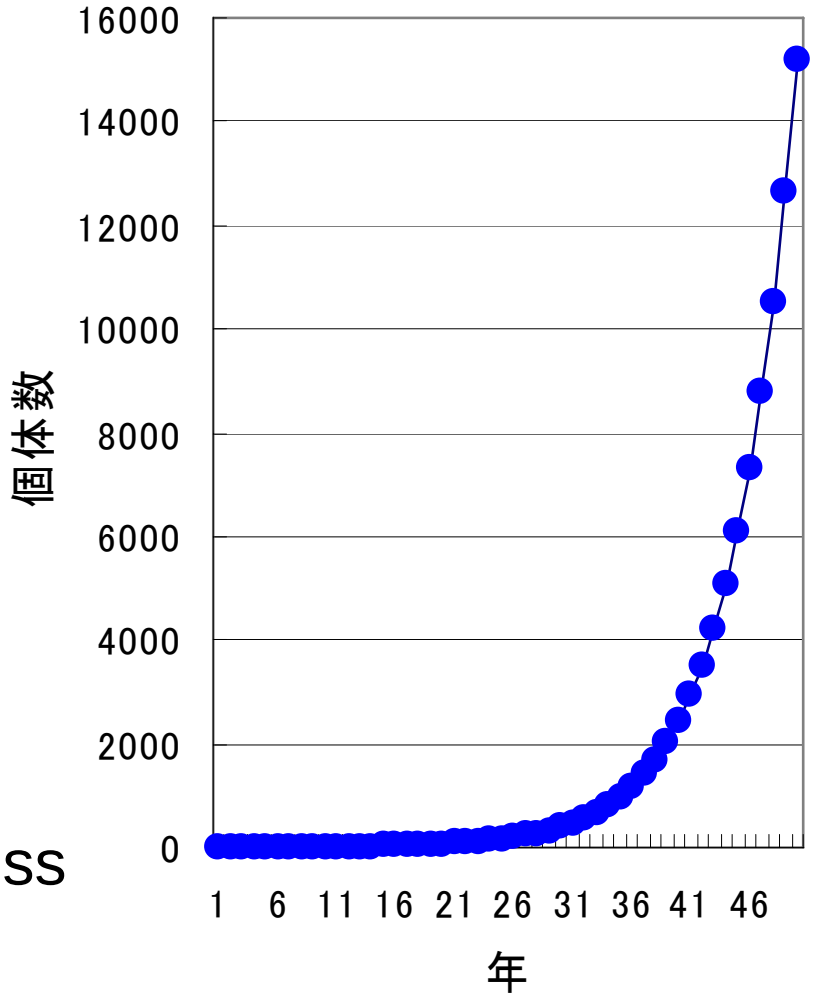
Average value depends on the definition of a population from which *n* individuals are sampled.

# Exponential growth 指数増加

$$\frac{dN}{dt} = rN$$

例：$N(0)=2$, $r=1.2$

$r$: intrinsic growth rate;
equivalent to average fitness

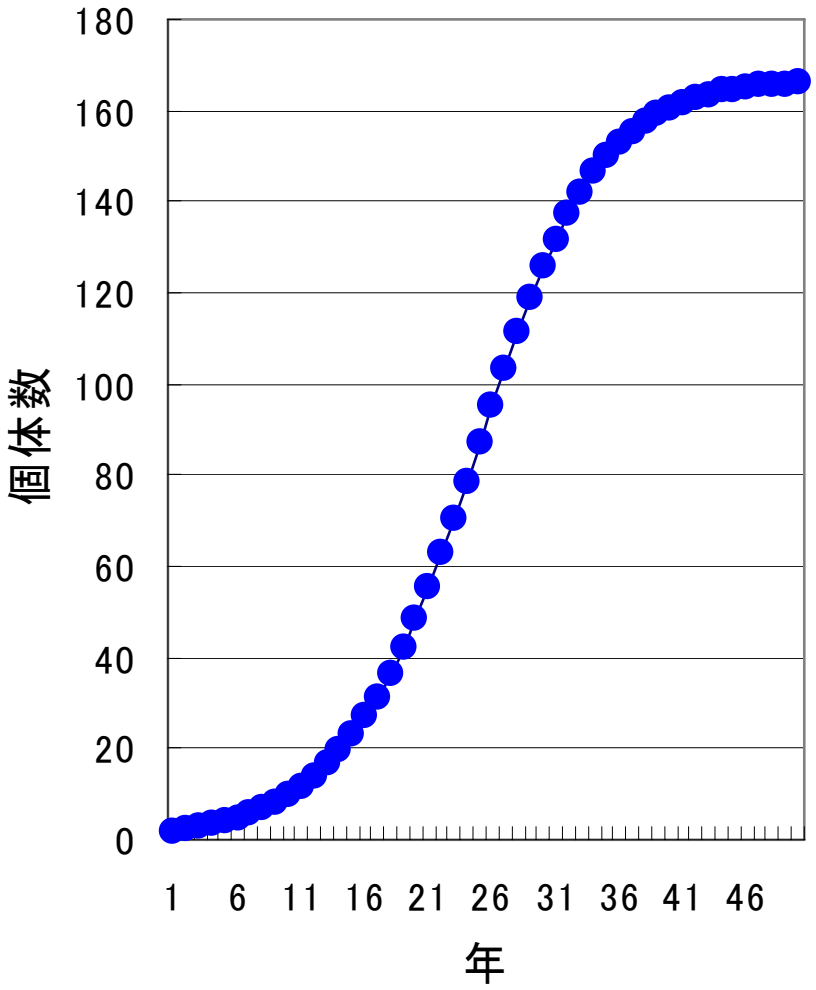


# Logistic growth ロジスチック成長

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

密度効果

$K$: 環境収容力
Carrying capacity



# Competition equation 競争方程式

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right)$$

# 競争方程式の平衡点

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1 + \alpha_{12} N_2}{K_1}) \geqq 0$$

種1が増える条件
Sp1 increases

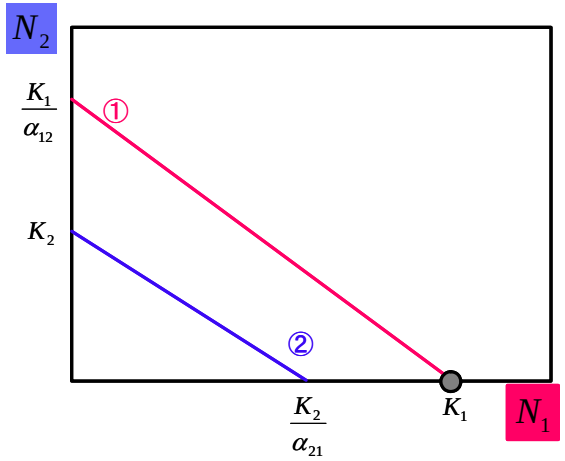
$$\Rightarrow \quad N_2 \leqq \frac{K_1}{\alpha_{12}} - \frac{N_1}{\alpha_{12}} \quad \cdots \quad ①$$

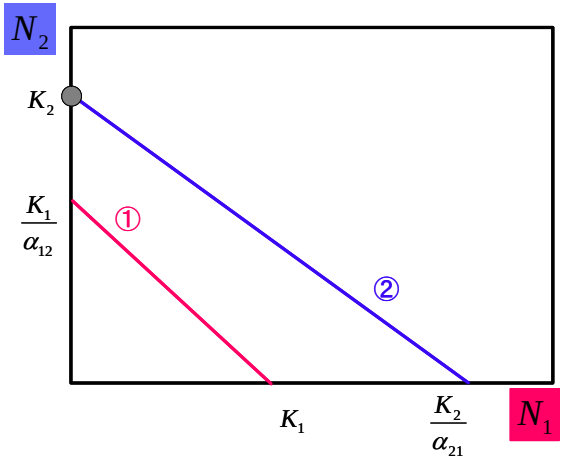
$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2 + \alpha_{21} N_1}{K_2}) \geqq 0$$

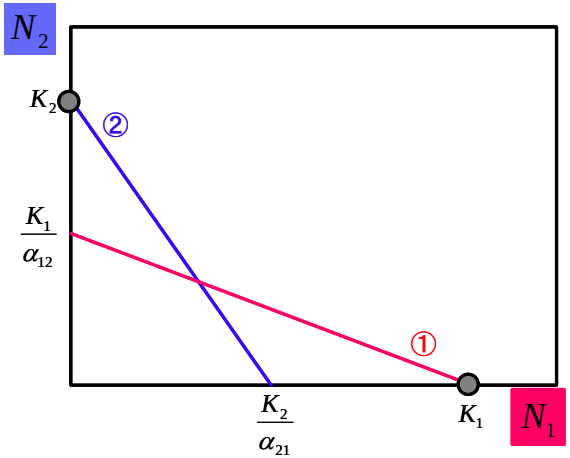
種2が増える条件
Sp2 increases

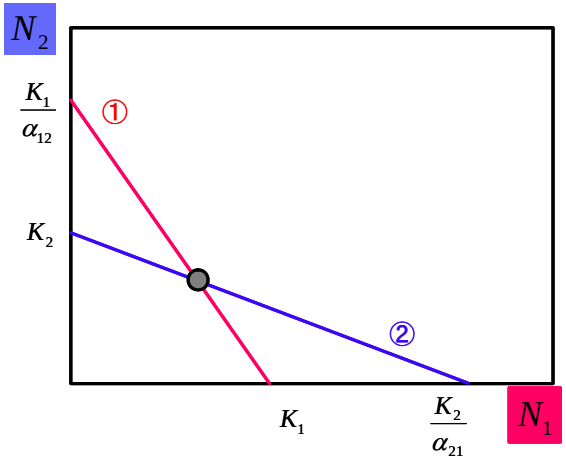
$$\Rightarrow \quad N_2 \leqq K_2 - \alpha_{21} N_1 \quad \cdots \quad ②$$

# Four cases 4つの場合

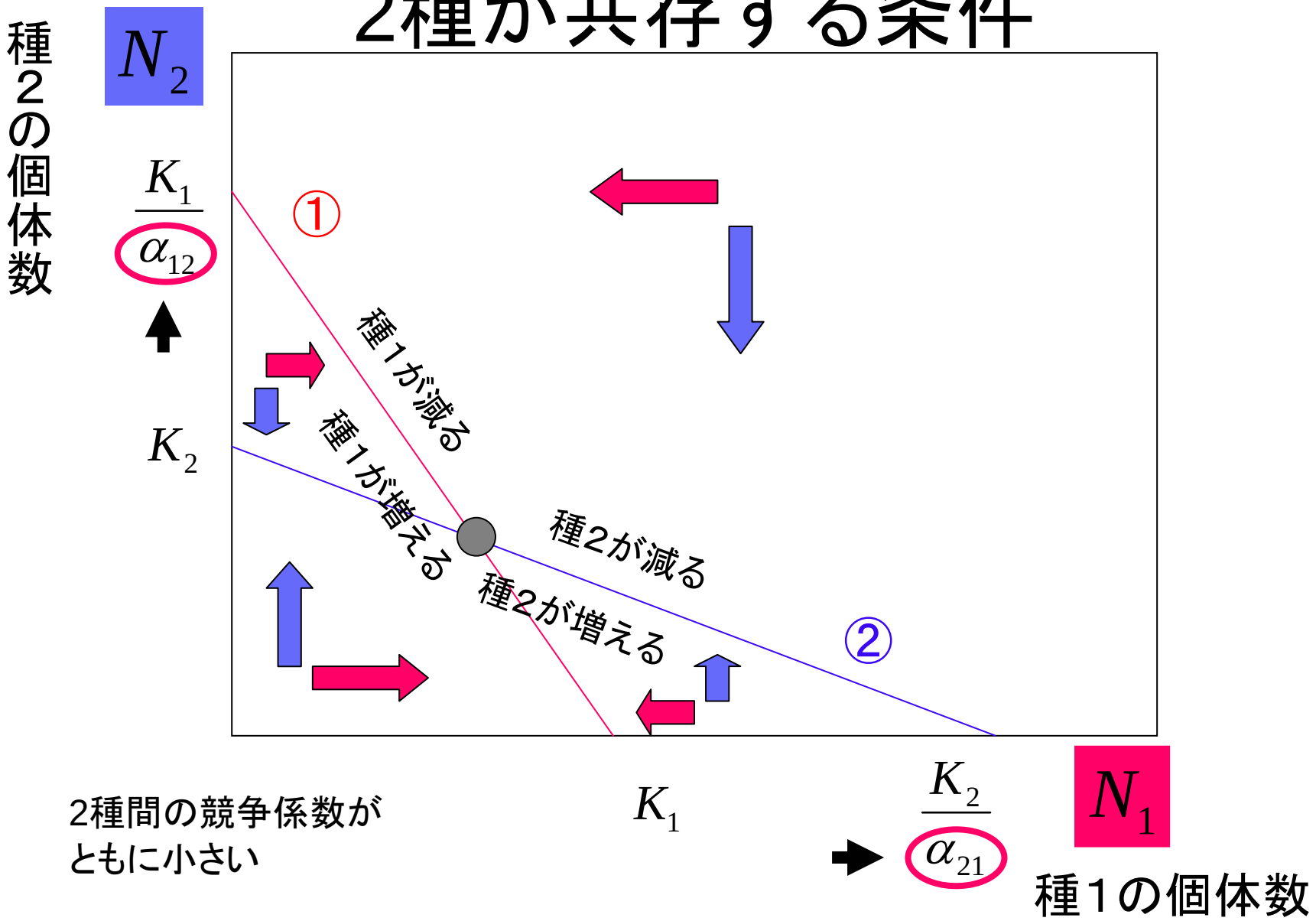


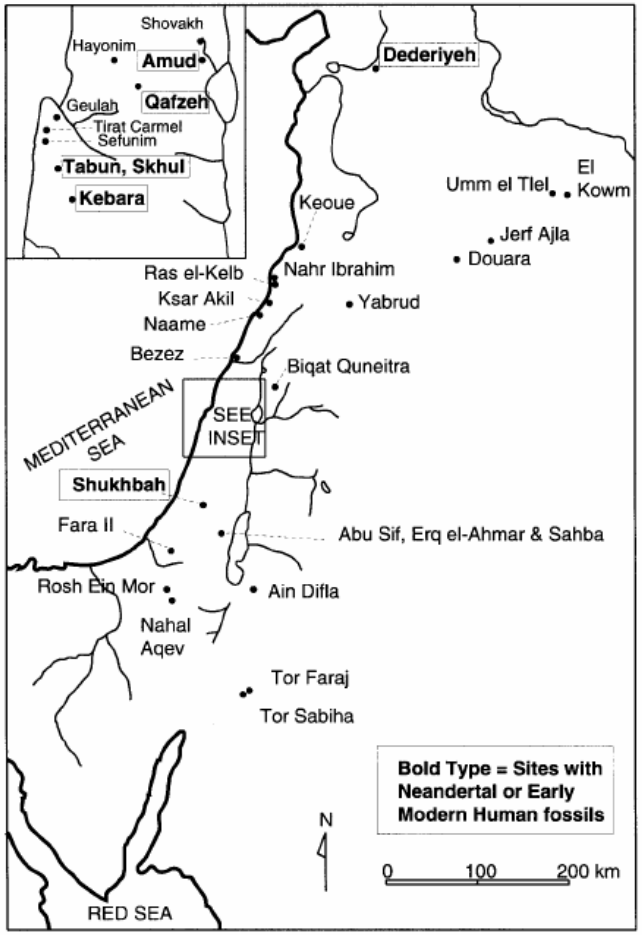



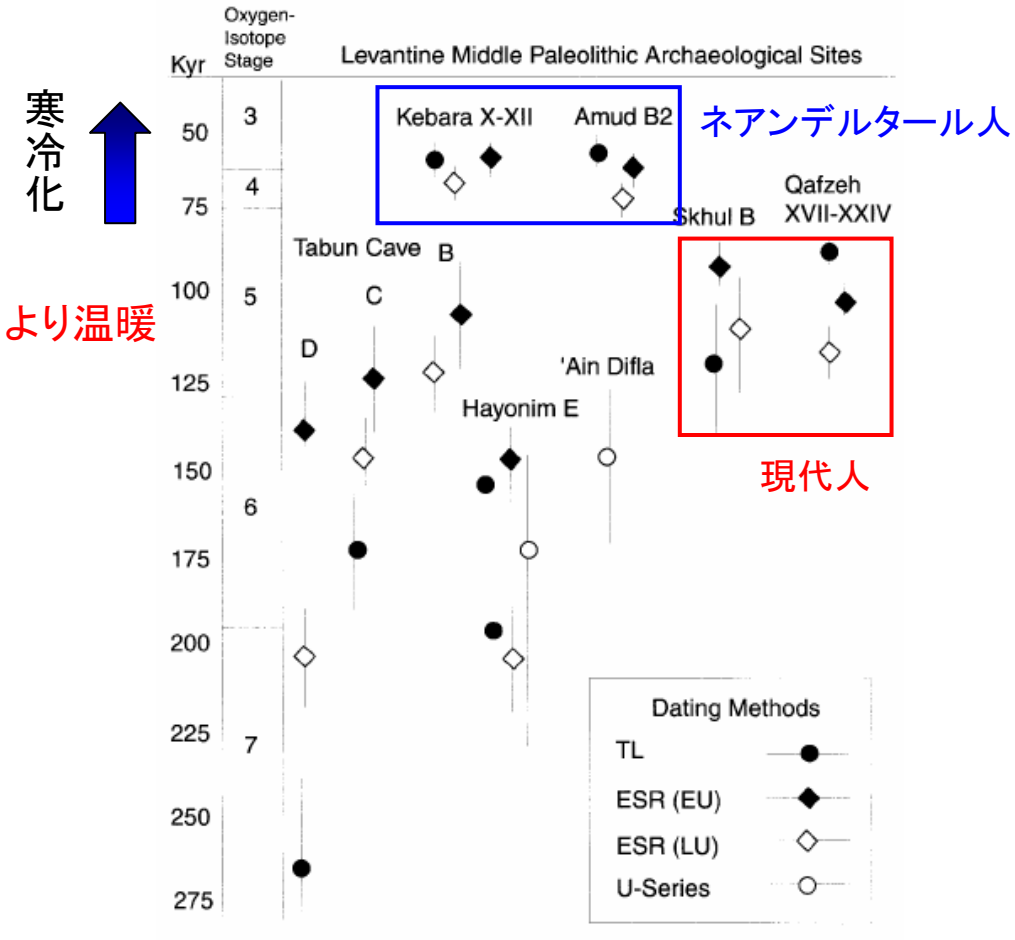
# Condition for co-existence
# 2種が共存する条件




2種間の競争係数が
ともに小さい

# レバントの化石人骨
# 現代人とネアンデルタール人の交代




Shea (2003) Neanderthals, competition, and the origin of modern human behaviour in the Levant.

# Homework: the case of mutualism

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1 - \alpha_{12} N_2}{K_1})$$

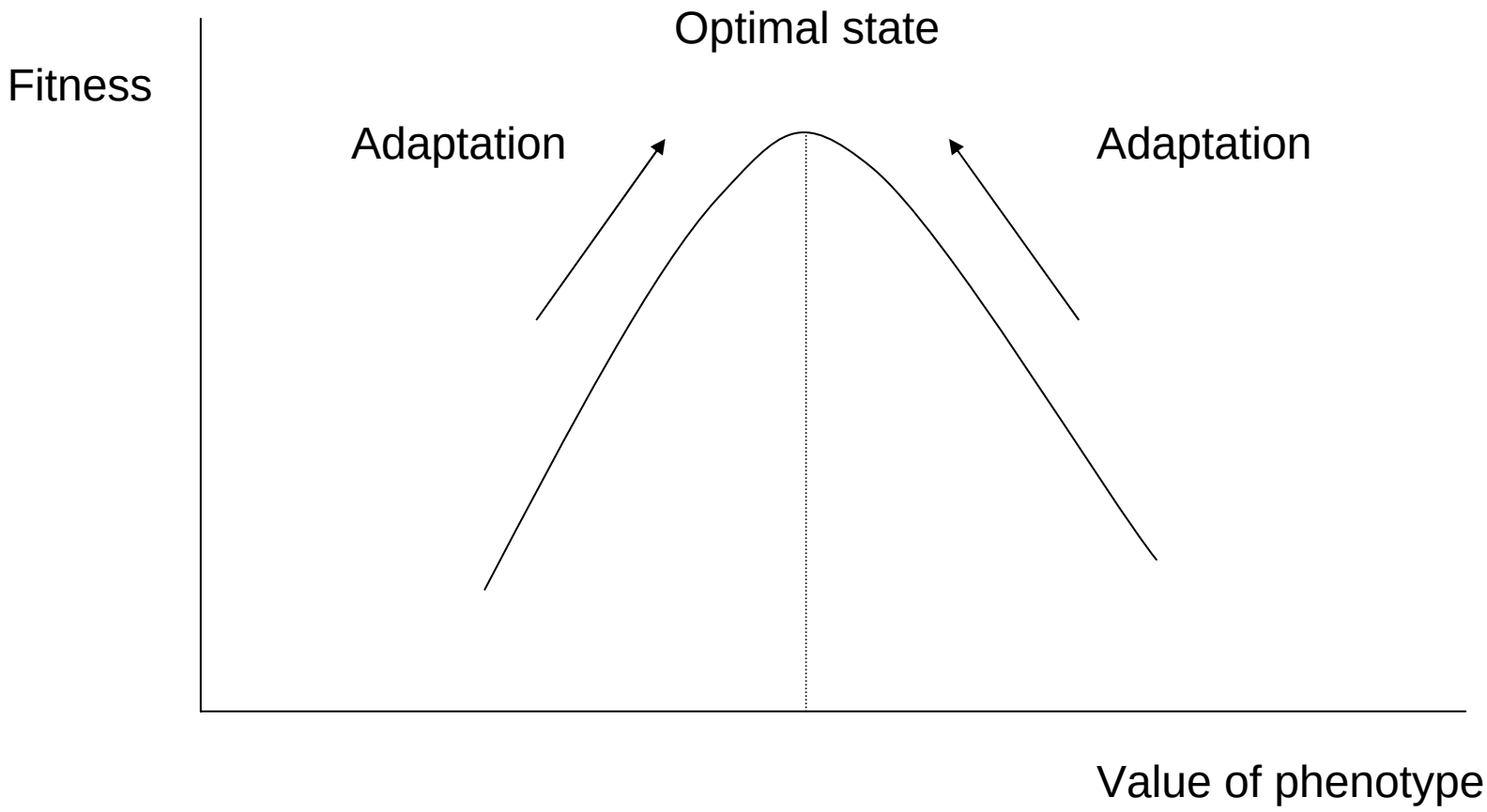
$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2 - \alpha_{21} N_1}{K_2})$$

The above equations describe changes of population size in two mutualistic species. Using these equations and graphic representations of population dynamics, derive and explain consequences of mutualism.

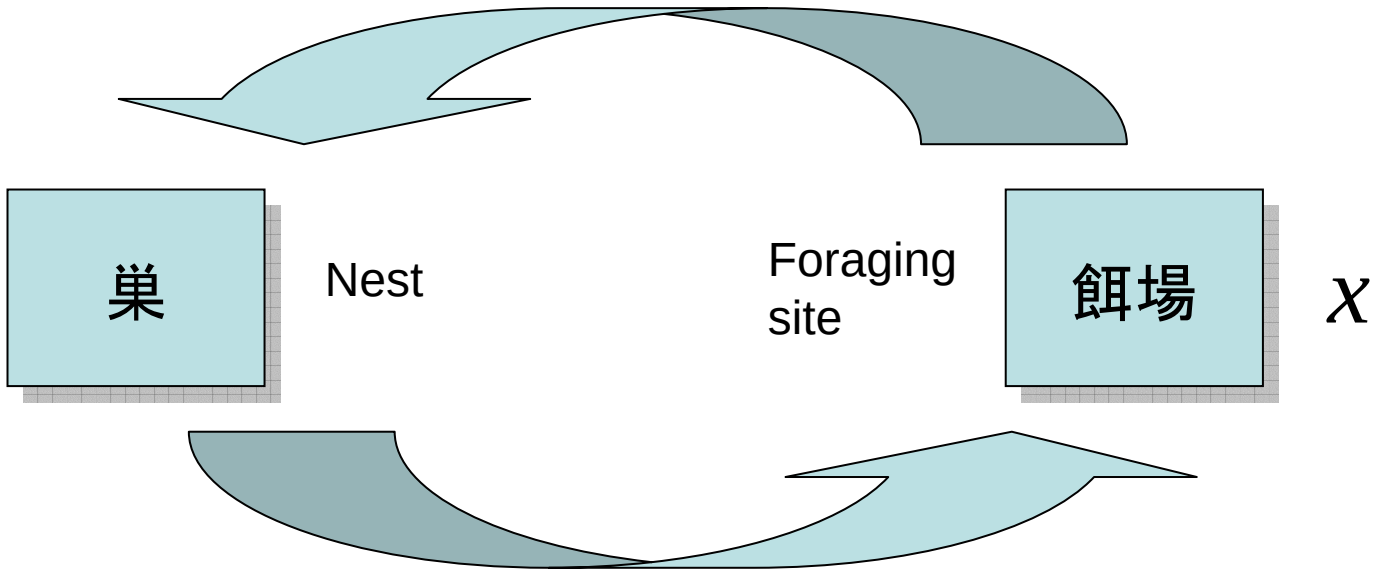
# Key points (1)

- Adaptation by natural selection occurs within a population
  - often through competition among individuals of the same population of the same species.
- Competition between species results in extinctions or coexistence
  - without any genetic changes

# Graphical representation of adaptation



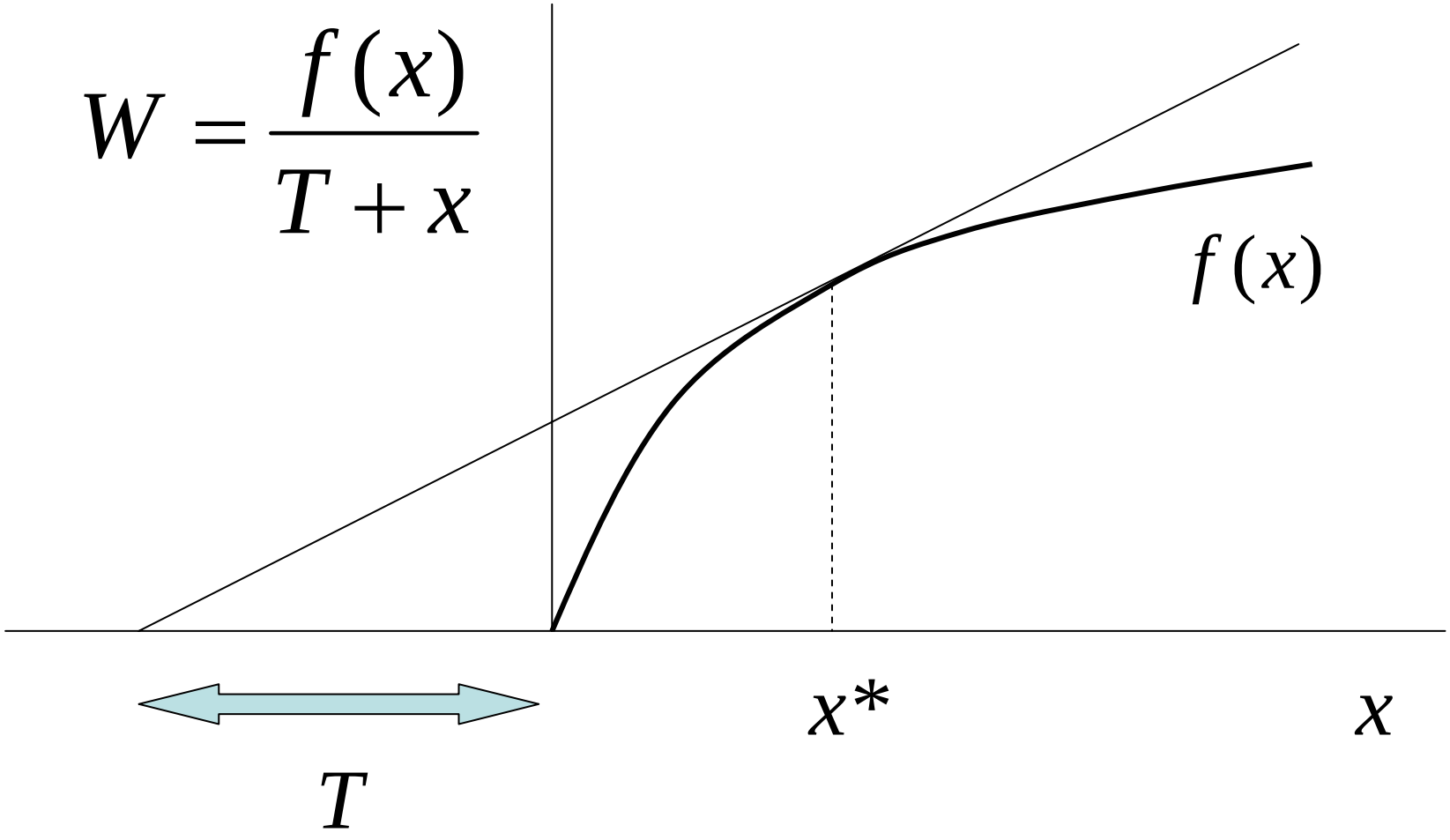
# Optimal foraging strategy
# 最適採餌戦略




$T$

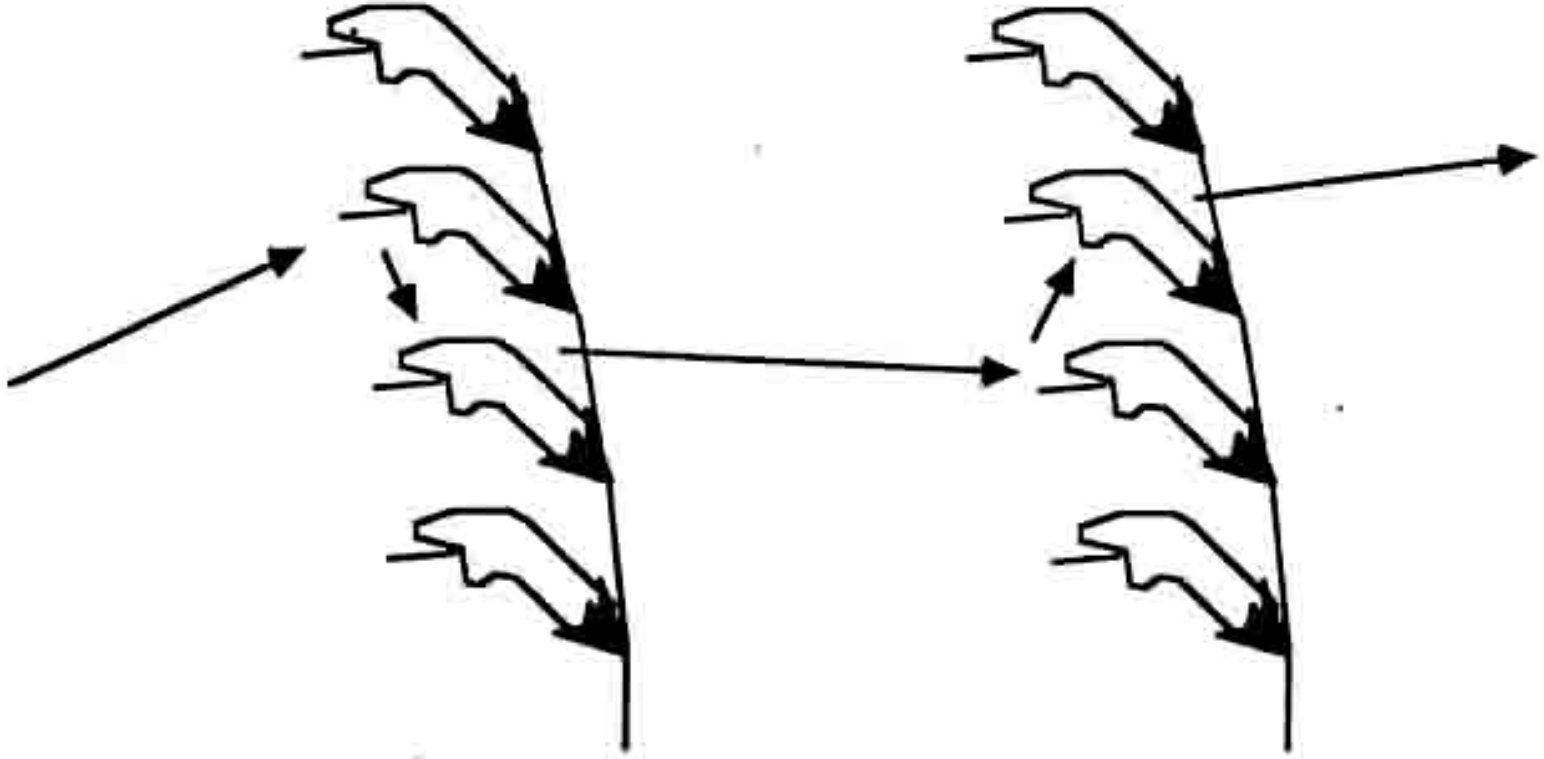
How long should an animal stay on a foraging site?

# Optimal foraging strategy
# 最適採餌戦略



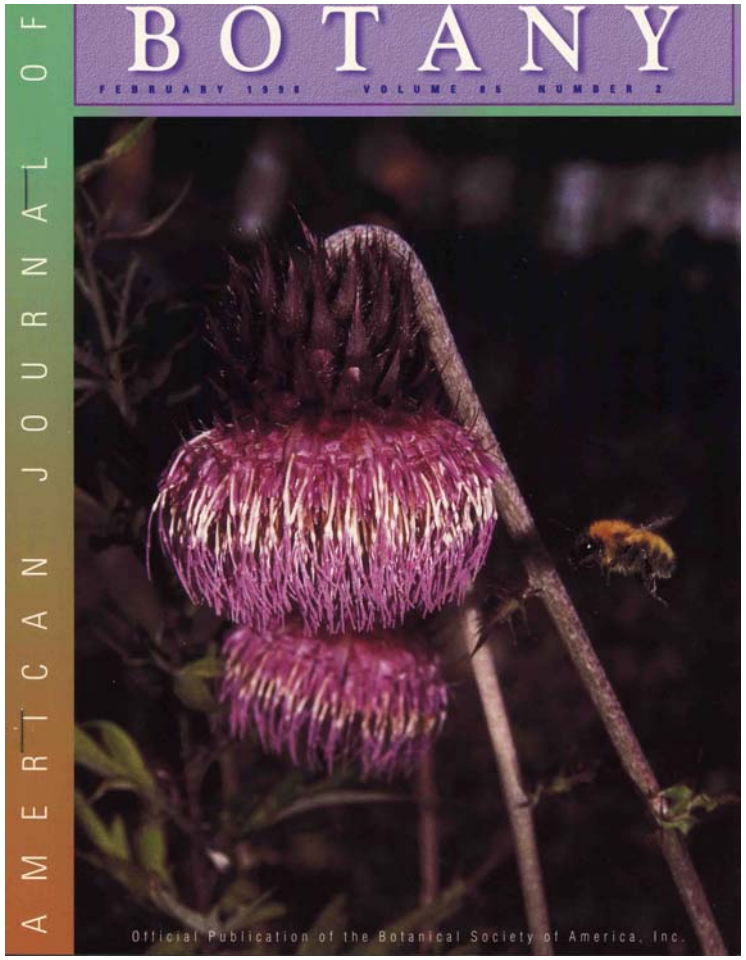
# Curious (apparently non-adaptive) behaviour of pollinators

Visit a few flowers per plant and fly to another plant



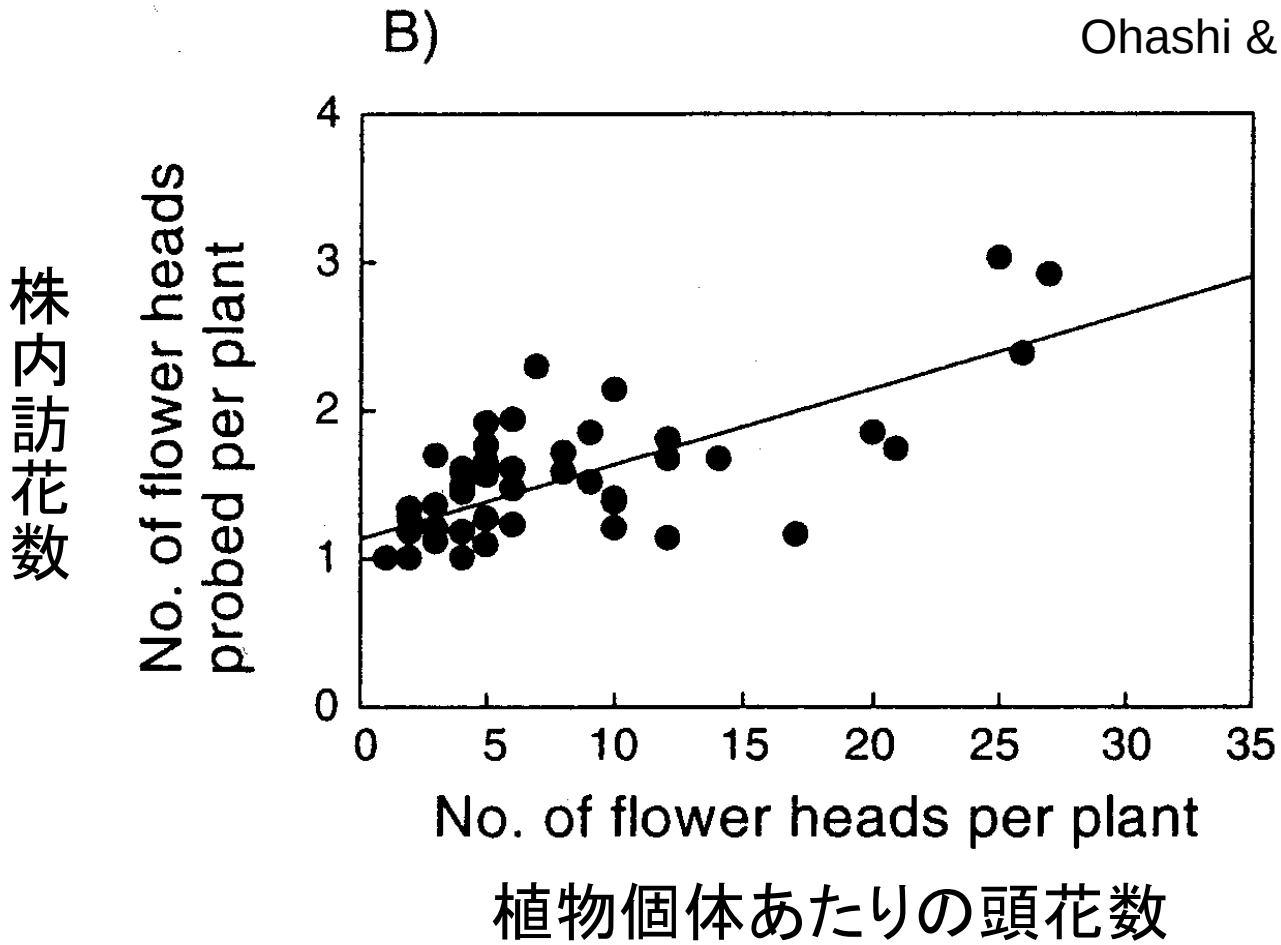
植物にとっては隣花受粉を少なくする有益な効果

# Cirsium purpuratum and bumblebees
# フジアザミとマルハナバチ

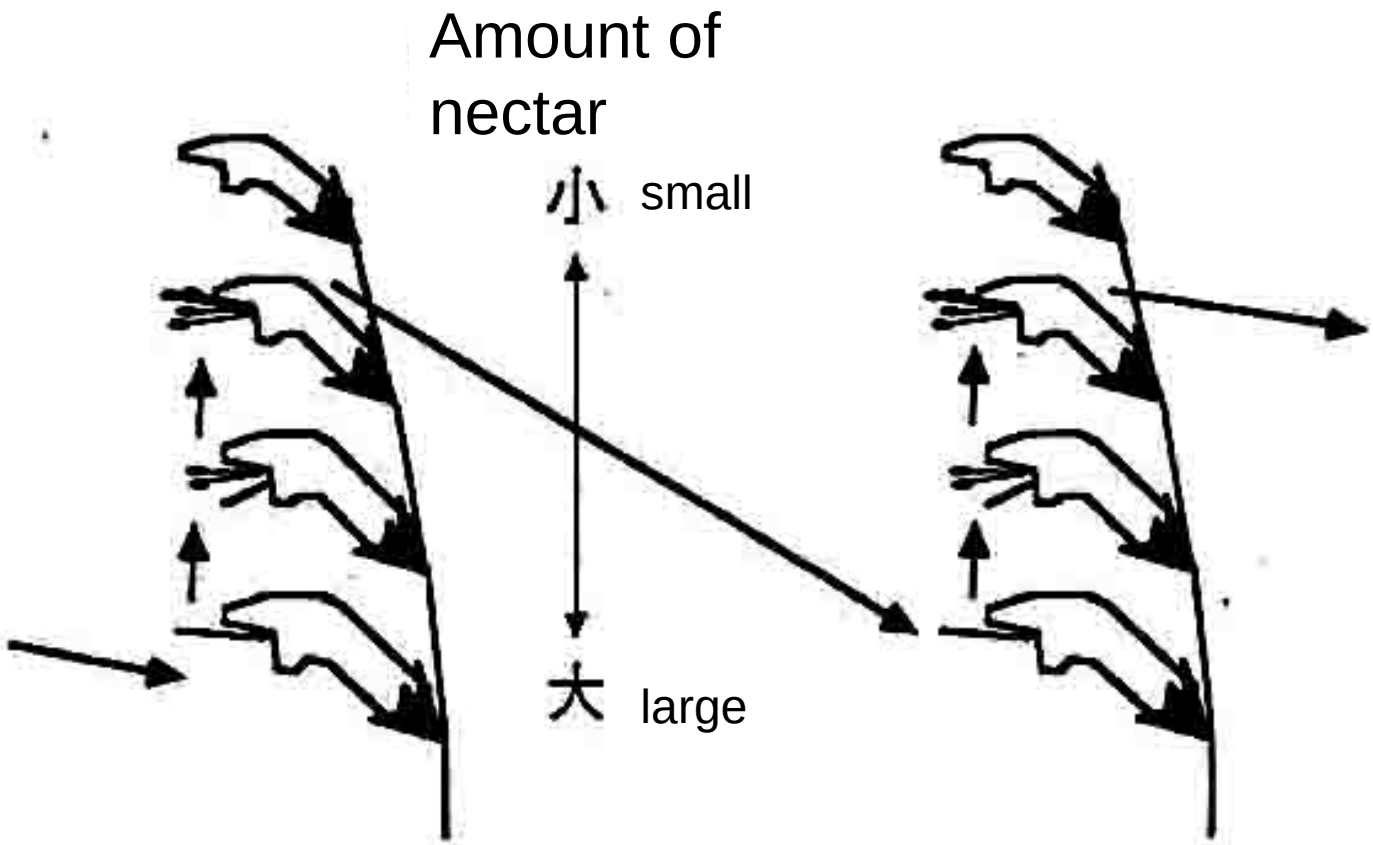



Ohashi & Yahara(1998)
Amer J Bot 85:219-224

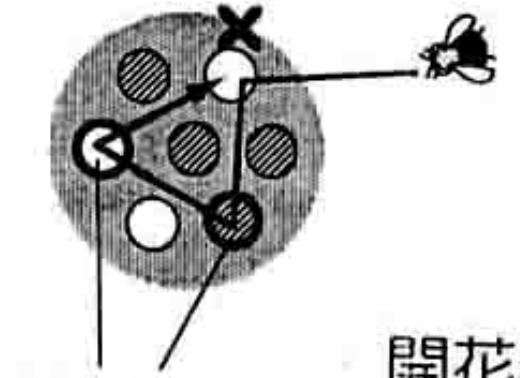
# フジアザミの花数とトラマルハナバチの株内訪花数の関係



Floral strategy to manipulate pollinator behaviour;
in the case that flower positions are easy to remember



# Ohashi & Yahara model



$G_{t+1} = \dfrac{Fp - n}{F - m}$

開花数

すでに出会った「アタリ」の花数

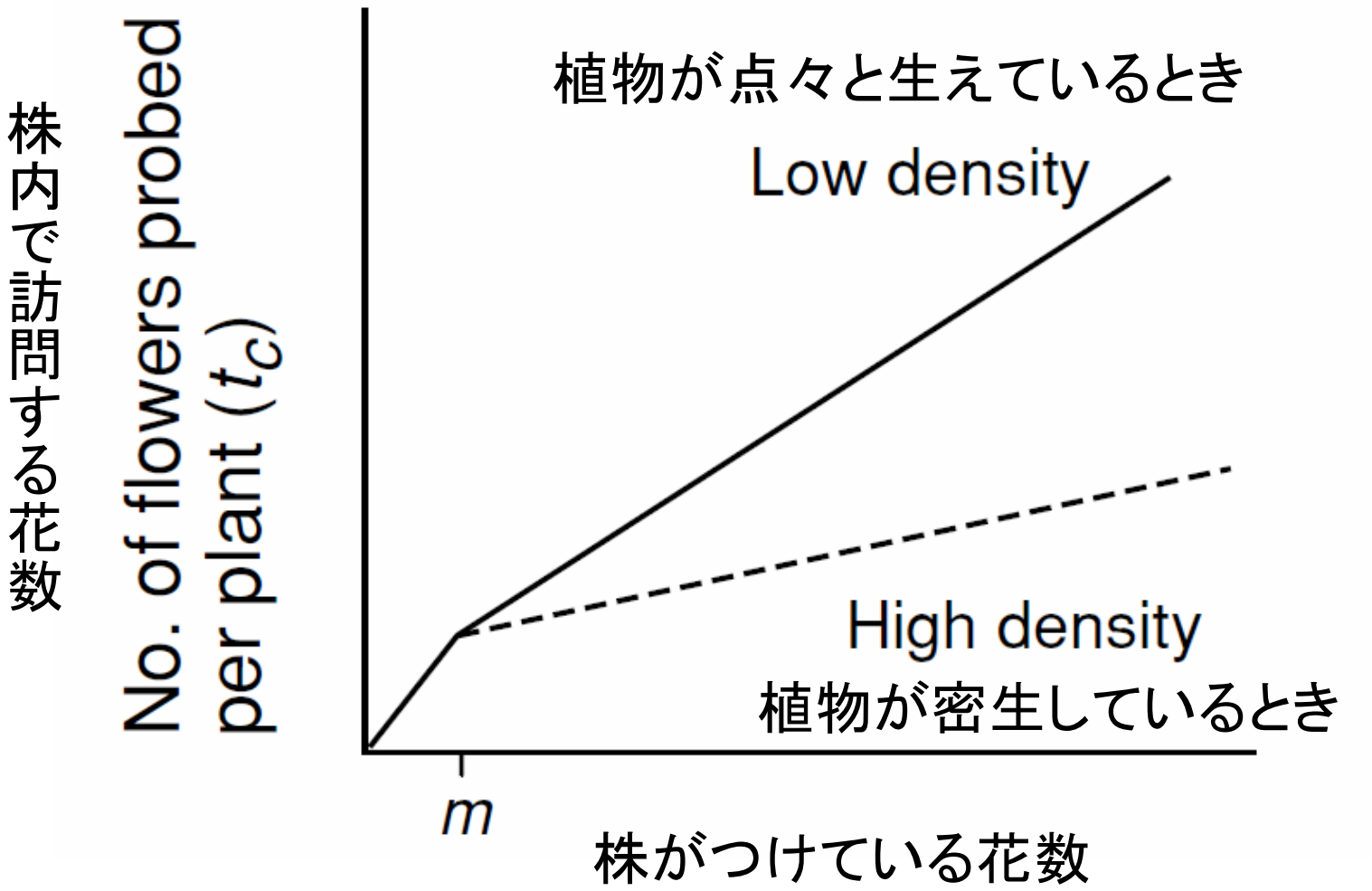
回避する $m$個の花

mは短期記憶の上限値

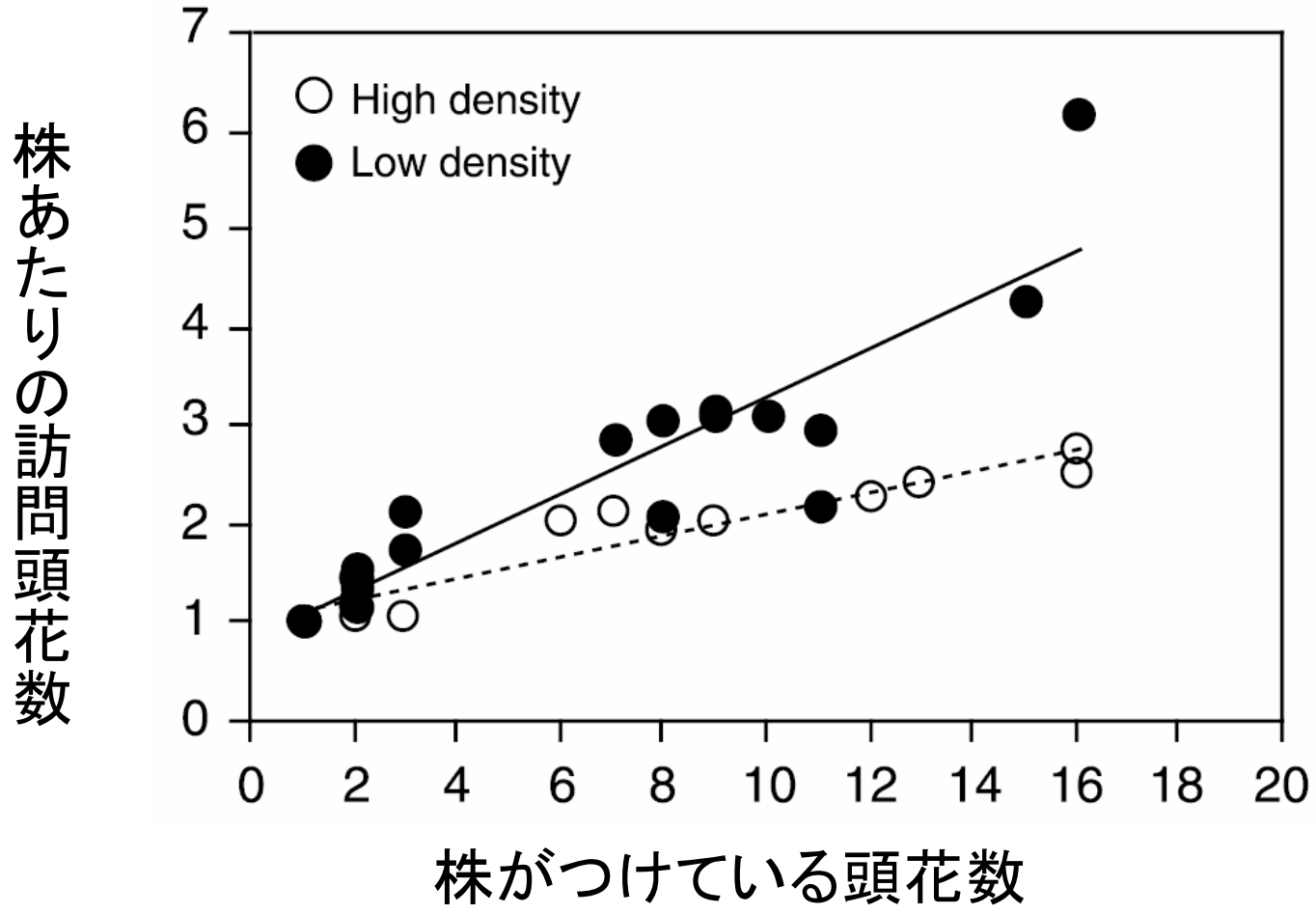
境界は $\dfrac{Fp - n}{F - m} = kp$

立ち去り条件は$G_{t+1}<kp$

# Predictions of Ohashi & Yahara model



# Observed bumblebee behaviors




Ohashi & Yahara (2002) Func Ecol 16: 492-503

# Stamen-removal experiment in Salvia nipponica

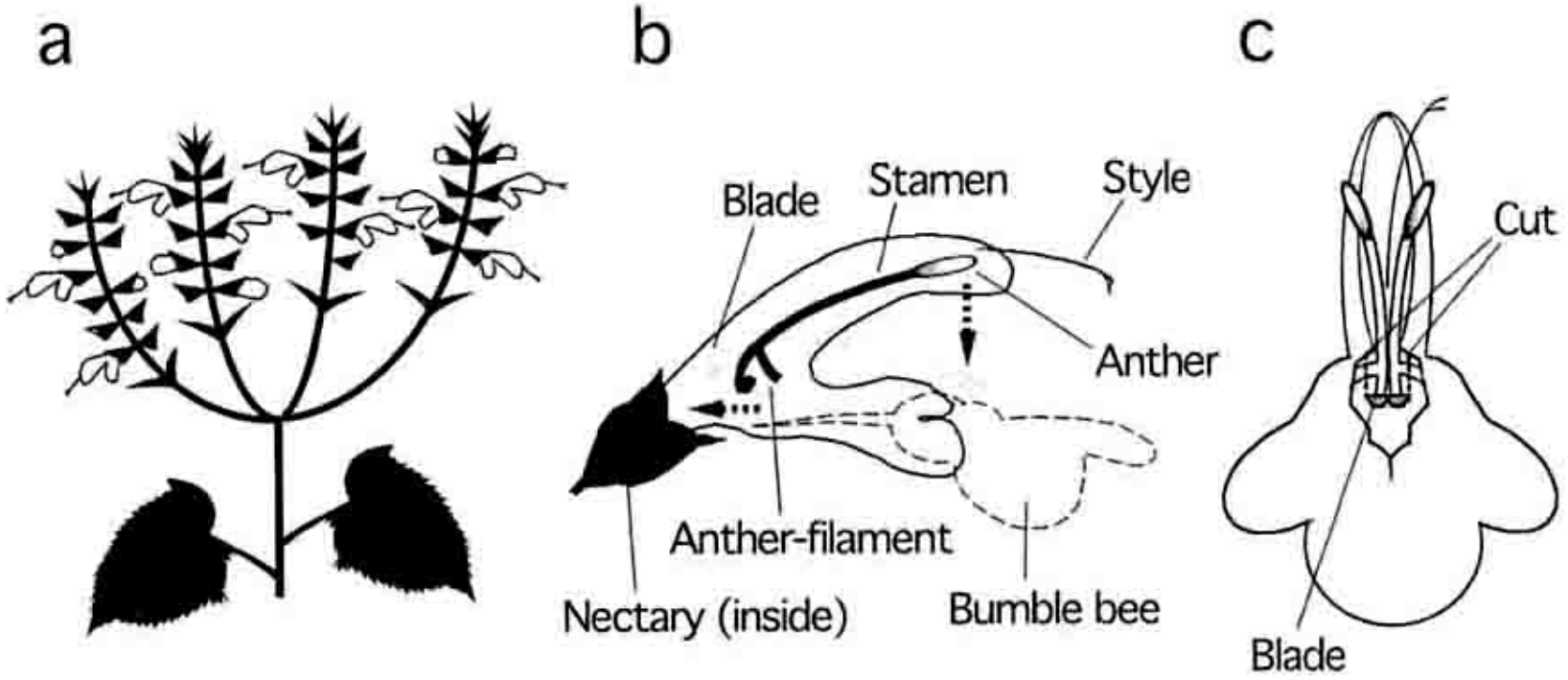



FIG. 1. Views of *Salvia nipponica*. (a) Flowering plant with four racemes, each of which bears two or three open flowers and no or two buds. (b) Half-section of a flower, showing the broadened lower end and the fertile anther cell on the upper end of one of the two fully developed anthers. Arrows and gray-colored stamen indicate the movement of the see-saw mechanism when a bee (dashed line) crawls into the flower. Immediately after the bee leaves the flower, the elastic stamen swings up into upper lips (see text). (c) Front view of a flower. The broken lines are the location of cutting for stamen-removal treatment.

Ohashi (2002)
Evolution
56: 2414-2423

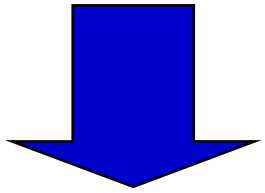
# 移動コスト（k）

Handling time

Time of within-plant movement

$$\frac{\text{花あたり処理時間}+\text{株内移動時間}}{\text{花あたり処理時間}+\text{株間移動時間}}$$

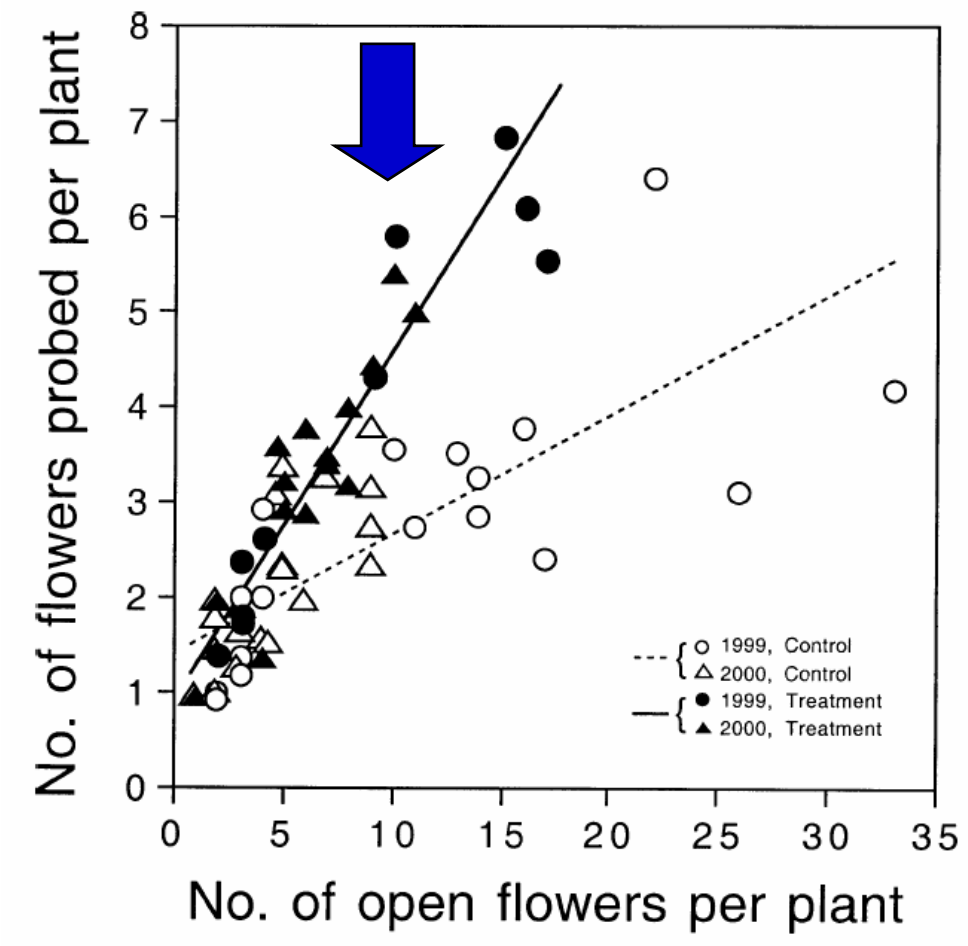
Time of between-plant movement



The larger the handling time is,
the sooner the bee leaves a plant.

# キバナアキギリへのマルハナバチの訪花行動

Flowers in which stamens were removed




株あたりの訪問花数

株あたりの花数

無処理の花

Control

Ohashi (2002)
Evolution
56: 2414-2423

# 切花をつかった訪問実験

# 好まれる頭花と嫌われる頭花

ほのかな甘い香り

くさった魚の臭い

# マルハナバチは自分の臭いを嫌う

Goulson et al. 2000



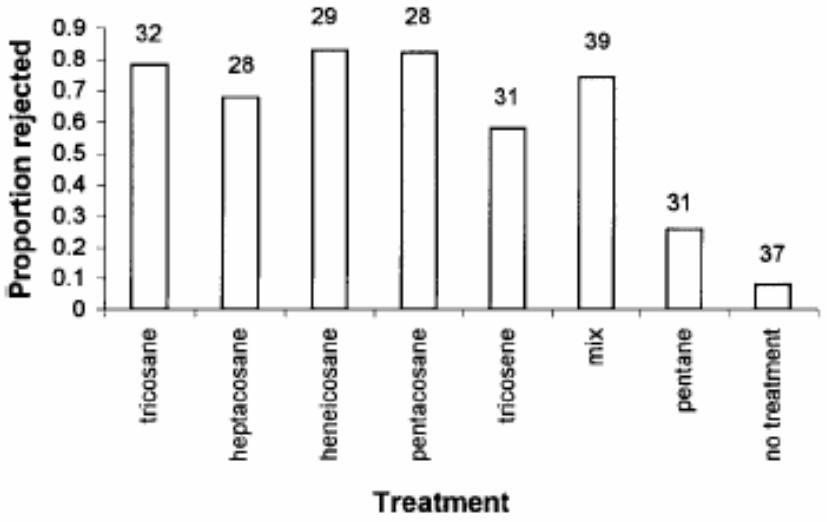



FIG. 3. The proportion of *B. lapidarius* workers rejecting *M. officinalis* flowers treated with $1 \times 10^{-12}$ $\mu$g of different compounds diluted in 5 $\mu$l of pentane, with 5 $\mu$l of pentane alone, or with nothing. Doses given are milligrams per flower. Numbers above the bars represent sample sizes.

ではなぜ同じ花にすぐに再訪問するのか？

# Key points (2)

- Prediction of optimal models is helpful to understand animal behaviour
  - Behaviors of many animals are consequences of adaptive evolution
- Pollinator behaviors are changed by floral traits
  - Plants can manipulate pollinator behaviors.
  - Pollinator behavior is a compromise between plant and pollinator adaptations.