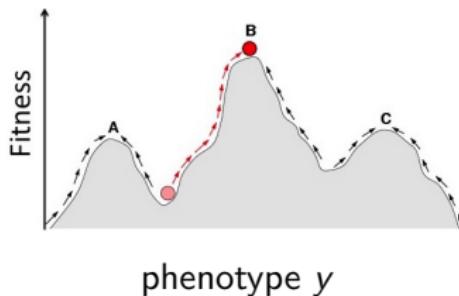


Adaptive dynamics (part 2: convergence stable strategies)

Recall: fitness landscape



$$S(y) = \left. \frac{\partial w(x, y)}{\partial x} \right|_{x=y} \quad w(x, y) \leq 1 \quad \forall x \in \mathcal{X}$$

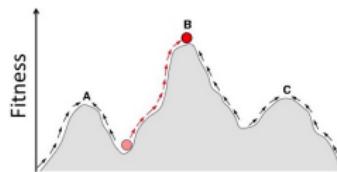
- ① An **uninvadable strategy** is a strategy that cannot be invaded by any alternative strategy in the strategy space \mathcal{X} .¹
- ② A **singular strategy** is a strategy nullifying the selection gradient (it satisfies $S(y) = 0$).

¹A local peak in the fitness landscape is a locally uninvadable strategy.

Adaptive evolution

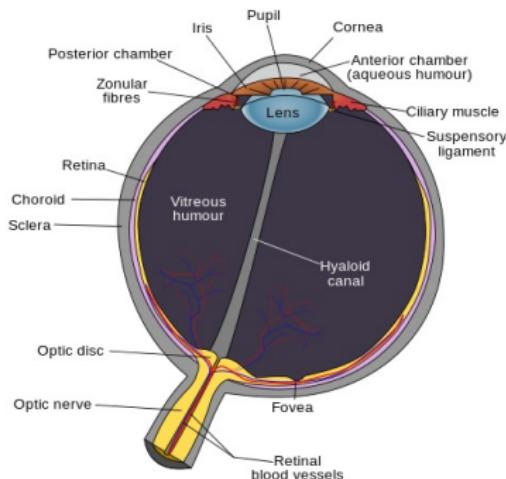
- Darwinian evolution is the process of random mutation plus non-random **cumulative** natural selection.
- It was postulated by Darwin to involve **small, step-by-step, transformation** of the phenotype of individuals in a population.
- This process results in individuals acquiring complex organic features that have the appearance of design and/or purpose.

“Natural selection is the blind watchmaker, blind because it does not see ahead, does no plan consequences, has no purpose in design” (Dawkins 1986).



The eye: the quintessential cumulatively evolved phenotype

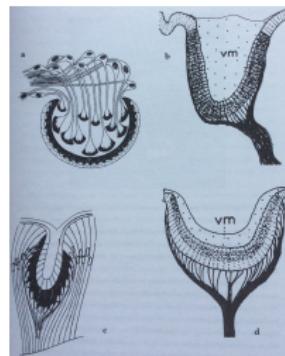
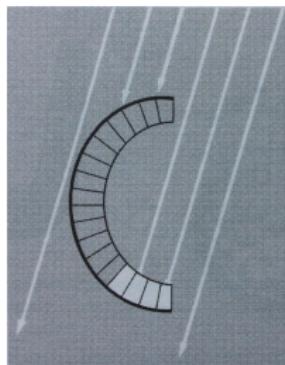
The eye is a remote sensing technology and a complex multidimensional adaptation.



- ① Dark pigment layer cells.
- ② Light sensitive cells.
- ③ Transparent cells (lens and vitreous humour).

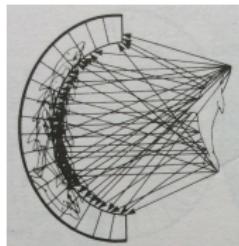
There are fitness benefits for sensing light without a full fledged camera “**a bad eye is better than no eye**”

- Showers of photons everywhere on earth.
- Sensing the direction of light is beneficial (e.g., locate food, escape predators). Cup eyes will be favored by selection and are prevalent in molluscs and worms.

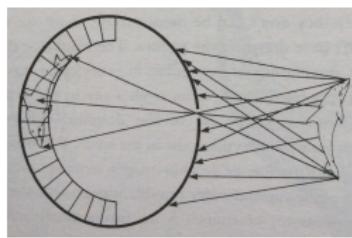


The path to enlightenment

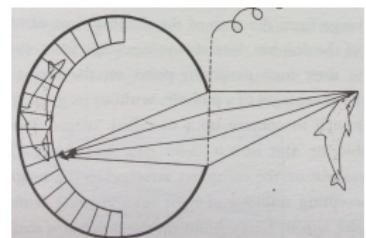
The eye evolved gradually by small changes.



Cup eye



Pinhole eye (with a pupil)

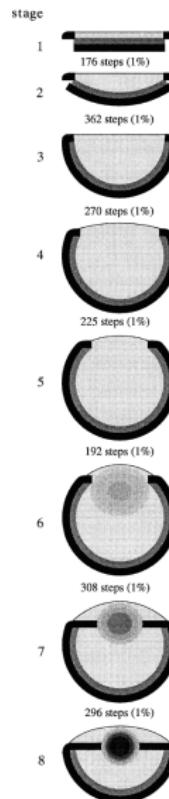


Lense eye (focuses light beams)

Any change on the way can be quantitative.

The time to enlightenment

- Starting with a layer of (1) dark pigments, (2) light sensitive cells, and (3) protective cells.
- About 1800 steps (at 0.005 change per generation) 360 000 generations required to evolve a good lens eye.
- What matters is that there is an infinitesimal advantage at each stage.



(Nilsson and Pelger 1994)

Has there been enough time to evolve all of organic complexity?

- Darwinian evolution works in small steps.
- Darwinian evolution works in “parallel”, beneficial mutations at one trait are retained after they become fixed, while beneficial alleles at other traits are being selected for.
- There has been plenty of time on earth to evolve eyes and brains.

But what are the conditions for gradual change? Can evolutionary change really be gradual in a world where there are many interactions? To address this we will return to our model with two alleles and formalize gradual evolution.

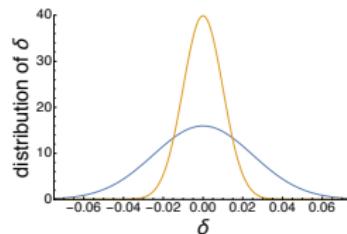
Under what condition does gradual evolution occur?

To understand gradual evolution we consider allele A whose carrier have phenotype x and allele B with phenotype y . We write the phenotype of A in terms of the phenotype of B as

$$x = y + \delta$$

or

$$\delta = y - x$$



Gaussian distribution $\exp\left(-\frac{\delta^2}{2\sigma_\mu^2}\right)$ with mean 0 and standard deviation or width $\sigma_\mu = 0.025$ (blue) and blue $\sigma_\mu = 0.01$ (yellow).

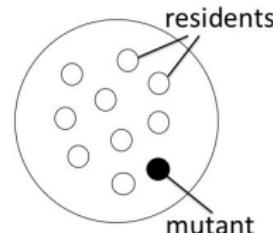
Here δ is the step size of the mutation.²

²Decades of empirical evidence show mutation step sizes are usually small for most mutations (the standard deviation σ_μ of the distribution of mutational effects is small).

The fitness of mutants and residents

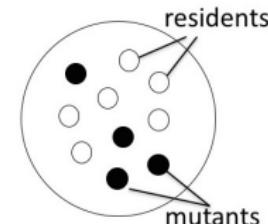
If there is only **one mutant** we have

- $w(x, y)$ fitness of a single mutant in a resident population.
- $w(y, y)$ fitness of a resident in a resident population.



If there are **several mutants** we have

- $w(x, \bar{y}(p))$ fitness of a single mutant in the population
- $w(y, \bar{y}(p))$ fitness of a resident in the population.



$\bar{y}(p)$ is the average phenotype of an individual from the population when the frequency of mutant A is p .

Allele frequency change

The change in the frequency of allele A is given by

$$\Delta p = \frac{p(1-p)s}{\bar{w}} \quad \text{with} \quad s = \underbrace{w(x, \bar{y}(p))}_{w_A} - \underbrace{w(y, \bar{y}(p))}_{w_B}$$

- The **selection coefficient** determines the direction of selection on allele A.
- The key assumption we now make is that the phenotypic difference

$$x = y + \delta$$

between mutant and resident is small (close to zero, $\delta \approx 0$).

Allele frequency change

By way of a Taylor series expansion of the selection coefficient around $\delta = 0$ (small mutation step size), we can write

$$s = w(x, \bar{y}(p)) - w(y, \bar{y}(p)) = \delta \underbrace{\frac{\partial w(x, y)}{\partial x} \Big|_{x=y}}_{S(y)} + \underbrace{O(\delta^2, p)}_{\text{remainder}}$$

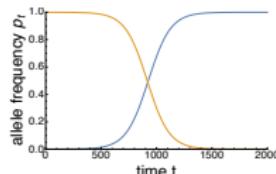
- The term $O(\delta^2, p)$ is a remainder of magnitude δ^2 . Suppose, $\delta = 0.1$, then $O(\delta^2, p)$ is of magnitude 0.01. Hence, for mutations with small step size it can be neglected.
- The selection coefficient measures the change in fitness resulting from phenotypic changes, and for small changes this is given directly by the selection gradient.³

³The selection gradient is expressed only in term of mutant and resident phenotype.

Allele invasion implies substitution

Dropping the remainder (assuming small δ), the change Δp in A frequency over one generation is

$$\Delta p = \frac{p(1-p)}{\bar{w}} \underbrace{\delta S(y)}_s$$



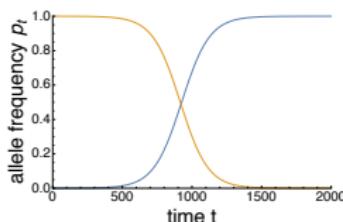
This holds at all frequencies p and implies that:

- ① For a mutant increasing trait value ($\delta > 0$) allele A is favored by selection if $S(y) > 0$ at all allele frequencies.
- ② For mutant increasing trait value ($\delta > 0$) allele A is disfavored by selection if $S(y) < 0$ at all mutant allele frequencies.

Allele invasion implies substitution

The change Δp in A frequency over one generation (for δ small) is

$$\Delta p = \frac{p(1-p)}{\bar{w}} \underbrace{\delta S(y)}_s$$

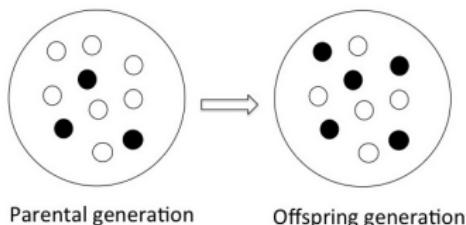


- This is equivalent to a model of constant selection with selection coefficient $s = \delta S(y)$. So the selection gradient predicts the direction of evolution, and **invasion implies substitution**.
- When a mutation invades the population we say that an **adaptive sweep** occurred.

Change in average phenotype due to adaptive sweeps

The change in the average phenotype \bar{y} in the population as the mutant sweeps through the population is⁴

$$\Delta\bar{y} = \bar{y}' - \bar{y} \\ = \delta\Delta p$$



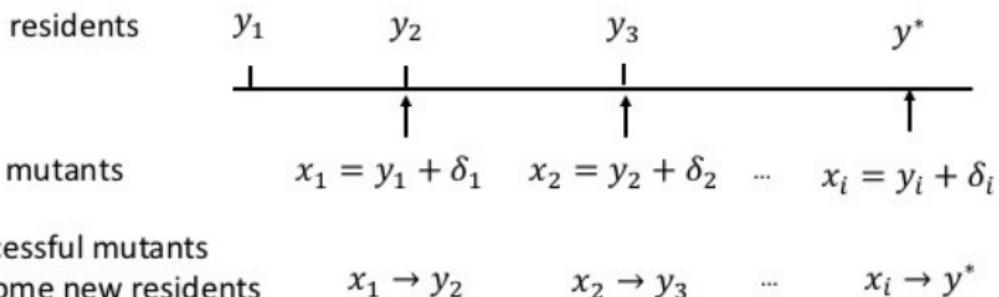
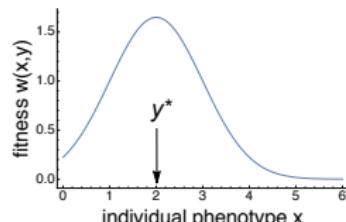
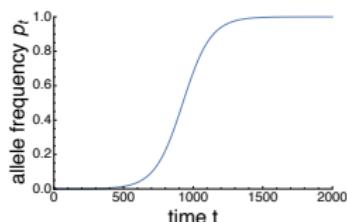
From the equation of allele frequency change we obtain

$$\Delta\bar{y} = V_y S(y) \quad \text{where} \quad V_y = p(1-p)\delta^2$$

is the phenotypic variance.

⁴In the two allele model the average phenotypes in the parental and offspring generations are, respectively $\bar{y} = px + (1 - p)y$ and $\bar{y}' = p'x + (1 - p')y$, where $x = y + \delta$.

Adaptive dynamics is a sequence of adaptive sweeps

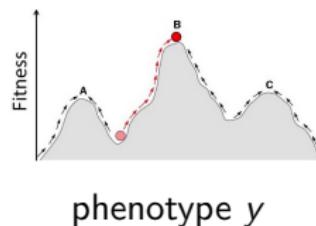


A sequence of adaptive sweeps will occur in the population, which will result in a gradual, step-by-step change in phenotype. The population “climbs” the slopes of the fitness landscape.

Change in average phenotype due to adaptive sweeps

As long as there is phenotypic variance produced by mutation, for any resident population with trait y , the phenotype will change according to

$$\Delta\bar{y} = V_y S(y)$$



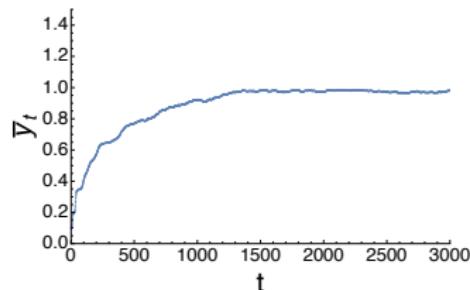
Hence, $S(y)$ generally describes the direction of evolution. An equilibrium point is reached when

$$\Delta\bar{y} = 0 \quad \implies \quad S(y) = 0$$

and any point y satisfying $S(y) = 0$ is a singular strategy.

Constant trait substitution

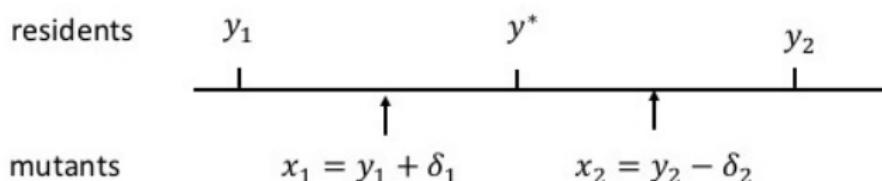
Average phenotype \bar{y}_t at time t under **stabilizing selection** with phenotypic optimum at $y^* = 1$.



In the presence of a constant influx of mutation we observe a gradual, step-by-step transformation of the phenotype, which results from mutant alleles constantly invading and replacing residents ones (**repeated adaptive sweeps**). This changes the phenotype until the singular strategy is reached. Hence, selection is stabilizing.

Convergence stability

Suppose y^* is a singular strategy that solves $S(y^*) = 0$.

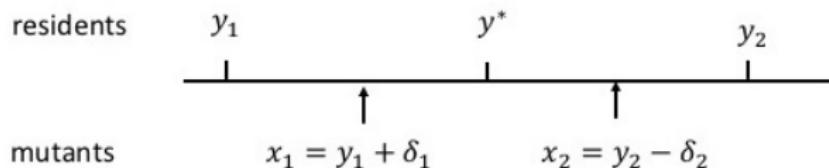
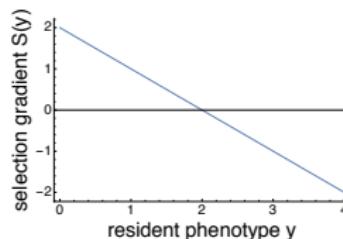
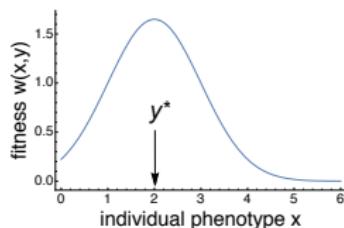


- Suppose that $S(y_1) > 0$. Then, for $y^* > x_1 > y_1$, the mutant x_1 invades and moves the population closer to y^* since $\delta_1 S(y_1) > 0$.
- Suppose that $S(y_2) < 0$. Then, for $y^* < x_2 < y_2$, the mutant x_2 invades and moves the population closer to y^* since $\delta_2 S(y_2) > 0$.

Then y^* is an attractor of the evolutionary dynamic.

Convergence stability

Suppose y^* is a singular strategy that solves $S(y^*) = 0$.



A strategy y^* is an attractor of the evolutionary dynamics if the selection gradient $S(y)$ is a monotonic decreasing function in y (downward sloping).

Convergence stability

A strategy y^* is an evolutionary attractor if

$$\frac{dS(y)}{dy} \Big|_{y=y^*} < 0 \quad S(y) = \frac{\partial w(x, y)}{\partial x} \Big|_{x=y}$$

- A strategy satisfying this condition is called a **convergence stable strategy**.
- An uninvadable strategy that is convergence stable is an **attractor** of the evolutionary dynamics and an end point of evolution.

Summary of adaptive dynamics: three type of strategies

- ① A **singular strategy** y^* satisfies $S(y^*)=0$.
- ② The evolutionary dynamics is attracted by **convergence stable strategies** (satisfying $dS(y)/dy|_{y=y^*} < 0$).
- ③ Convergence stable strategies can be (locally) **uninvadable strategies** (satisfying $\partial^2 w(x, y)/\partial x^2|_{x=y=y^*} \leq 0$).⁵



⁵In figure, convergence stable strategies are locally uninvadable. But real fitness landscapes are dynamic (they change as evolution occurs) and there is no general reason that convergence stable strategies are uninvadable.

Two applications under competition for resources

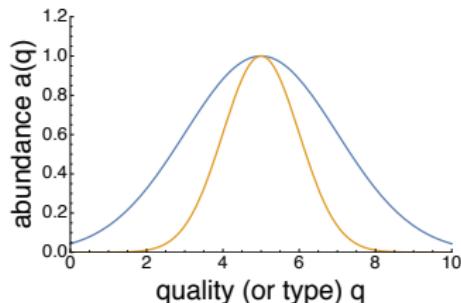
We will exemplify these ideas and provide two interesting applications of adaptive dynamics to the evolution of competitive traits:

- ① Exploitation competition leading to disruptive selection and **evolutionary branching**.
- ② Interference competition leading to directional selection and **evolutionary suicide**.

Resource abundance distribution

Suppose resource type or quality follows a dome shaped (gaussian) abundance distribution

$$a(q) = \exp\left(-\frac{(q - q_{\max})^2}{2\sigma_a^2}\right)$$



Parameters $q_{\max} = 5$ with $\sigma_a = 2$ (blue curve) and $\sigma_a = 1$ (yellow curve).

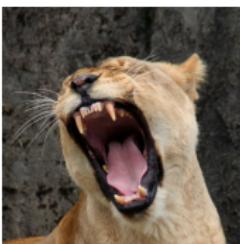
- Here q_{\max} is the type of the resource that has maximum abundance in the population and σ_a is the resource width.
- Essentially any resource comes in different types (or qualities) and has some abundance distribution.

Phenotype matching resources use

We assume that a **one-dimensional phenotypic trait** maps directly on the resource axis and describes how efficient individuals are at extracting resources.



Humming birds can extract nectar only from specific flowers (phenotype is beak shape).



Lions track medium sized prey (phenotype is jaw size).



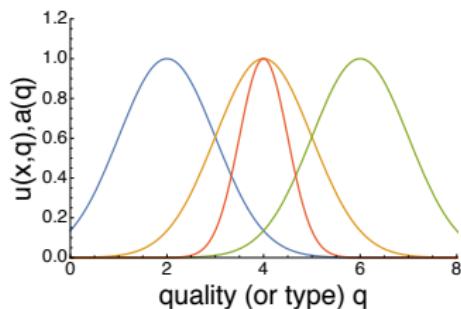
Bushmen often track antelopes they exhaust by jogging (phenotype is endurance).

The phenotype describes the match between the feeding or hunting apparatus of the individual and the structure of the resource.

Resource utilization niche

We assume that the **resource utilization function** at exploiting resource of type q of a focal individual with phenotype x is also dome shaped

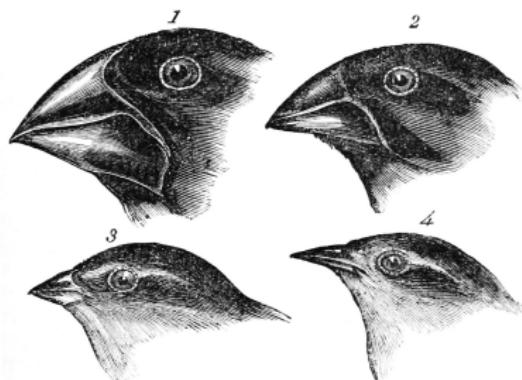
$$u(x, q) = \exp\left(-\frac{(x - q)^2}{2\sigma_u^2}\right)$$



Parameters $\sigma_u = 2$ and from left to right $x = 4$, $x = 6$, and $x = 6$. The resource abundance curve (in red) has $q_{\max} = 4$ and $\sigma_a = 2$.

Here σ_u is the **resource utilization width** and describes how generalist an individual is.

Example: Darwin's finches



1. *Geospiza magnirostris*.
3. *Geospiza parvula*.

2. *Geospiza fortis*.
4. *Certhidea olivacea*.

- Darwin's finches (living on Galapagos island) are a group of about fifteen species of passerine birds
- They have a diversity in beak form and function adapted to different food sources (seed types) that expand their feeding opportunity and limit competition.

Exploitation competition: fitness

Because of competition for resources, the share of resources of type q obtained by a single individual with phenotype x in a resident y population is assumed to be given by its relative efficiency at extracting resources

$$r_e(x, y, q) = \frac{u(x, q)}{u(y, q)}$$

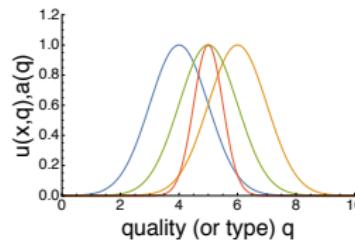
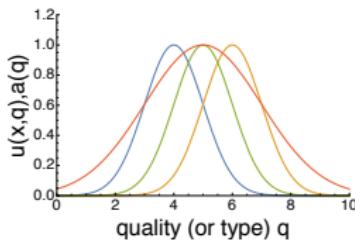
The fitness of an individual with phenotype x in a resident y population is assumed to be proportional to the average share of resources it obtains over the abundance distribution⁶

$$w(x, y) = k \int_{-\infty}^{\infty} a(q) r_e(x, y, q) dq$$

⁶The constant $k = k(y)$ depends on the equilibrium resident population size $n^*(y)$ and takes density-dependent competition into account, but this does affect the results because selection is density-independent so we can just treat k as constant.

Which resource type should individuals exploit?

Should individuals exploit the most abundant resource?

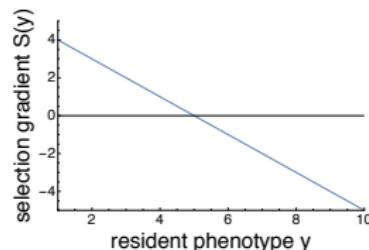


Parameters $\sigma_u = 1$ and $x = 4$ (blue), $x = 5$ (green), and $x = 6$ (yellow). Resource abundance (red) $q_{\max} = 5$, and $\sigma_a = 2$ (left panel) and $\sigma_a = 0.5$ (right panel).

Exploitation competition: the selection gradient

The selection gradient on the resource using phenotype is⁷

$$S(y) \propto \frac{q_{\max} - y}{\sigma_u^2}$$



Parameters: $q_{\max} = 5$ and $\sigma_u = 1$

When $y < q_{\max}$, increasing the trait value increases fitness, while if $y > q_{\max}$, increasing the trait value decreases fitness.

This suggests that **selection is stabilizing**.

⁷The symbol \propto means equal to up to a constant of proportionality.
Proportionality constants do not affect the direction of evolution.

Exploitation competition: the singular point

The single point of the system (satisfying $S(y^*) = 0$) is

$$y^* = q_{\max}$$

This is also a convergence stable point owing to the fact

$$\left. \frac{dS(y)}{dy} \right|_{y=q_{\max}} < 0$$

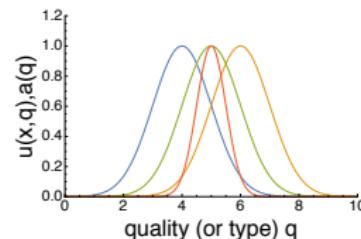
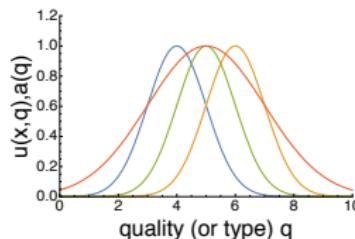
Hence exploiting the most abundant resource is an attractor point of the evolutionary dynamics. But is this point also uninvadable?

Exploitation competition: second-order condition

The second-order condition of uninvadability is

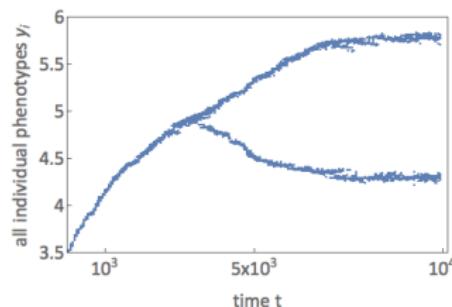
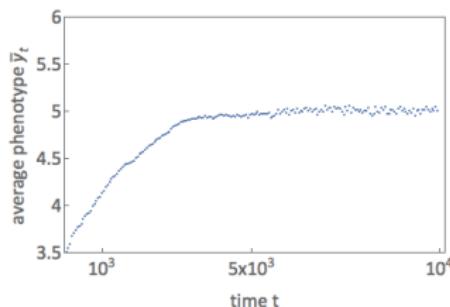
$$\left. \frac{\partial^2 w(x, y)}{\partial x^2} \right|_{x=y=q_{\max}} \leq 0 \implies \sigma_a \leq \sigma_u$$

- The point $z = q_{\max}$ is invadable if $\sigma_a > \sigma_u$. Namely, if the width of the resources abundance distribution is wider than the width of the resource utilization curve.
- This means that selection is disruptive at the convergences stable strategy. We have reached a fitness minima.



The resource abundance curve is in red.

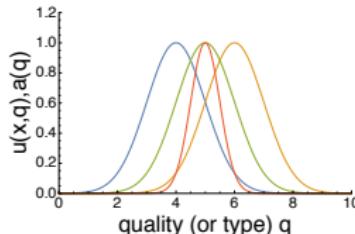
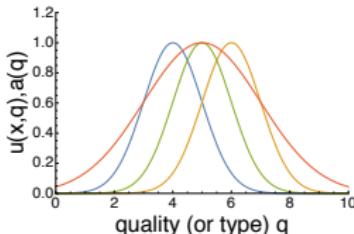
Convergence to convergence stability and branching



Parameters are $n = 1000$, $q_{\max} = 5$, $\sigma_a = 2$, $\sigma_u = 1$, $\bar{y}_0 = 1$, $\mu = 10^{-3}$ (mutation rate) and $\sigma_\mu = 0.05$ (mutation step-size standard deviation).

- The population first evolves towards the convergence stable strategy as predicted: $y = 5$.
- But the fitness landscape is changing as evolution proceeds and progressively transforms into a fitness valley. The population splits into a bimodal distribution. Selection becomes disruptive and polymorphism (diversity) is maintained.

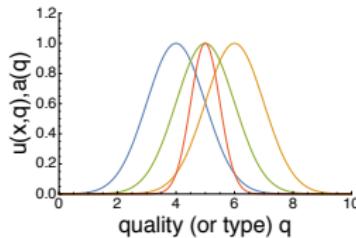
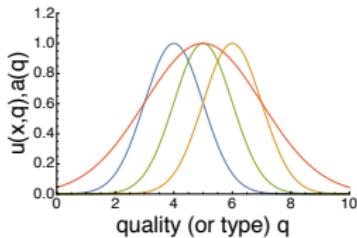
Maintenance of diversity if $\sigma_a > \sigma_u$



Parameters $\sigma_u = 1$ and $x = 4$ (blue), $x = 5$ (green), and $x = 6$ (yellow). Resource abundance (red) $q_{\max} = 5$, and $\sigma_a = 2$ (left panel) and $\sigma_a = 0.5$ (right panel).

- If everybody plays $y^* = q_{\max}$ competition is fierce and it pays to exploit another less abundant resource if there is not too much overlap in resource use (left panel with $\sigma_a > \sigma_u$ leading to **disruptive selection** and coexistence).
- If there is much overlap in resource use (right panel $\sigma_u > \sigma_a$), then there is no point of exploiting less abundant resource.

Limiting similarity



Left panel coexistence between strategies ($\sigma_a > \sigma_u$), right panel only one strategy will dominate ($\sigma_u > \sigma_a$).

- There is a limit to the similarity between strategies (“**limiting similarity**”) for diversity coexistence. This limit to similarity ultimately comes from trade-offs.
- This idea of limiting similarity and the resulting disruptive selection underlies much of the ecological diversification observed in the natural world.

Interference competition

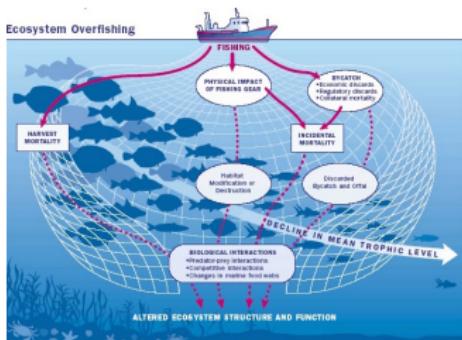
Animals often fight and interfere with each other.



- Investment into competition results in more resources acquired individually but can have deleterious side effects.
- Some deer have such big antlers (thought to be investments into competition to attract mates) that it hinders them on other activities.

Tragedy of the common

Investment into competitive ability (catchability) for fish can have deleterious side-effects. Decrease of the common good.



- There is a trade-off between individual and common benefits.
- Many past societies collapsed because they endogenously created environmental problems (Diamond 2005).

Trade-off between individual and population benefit

The number of resources extracted by a single individual with phenotype x in a resident population where individuals at large express trait y is assumed to be given by⁸

$$w(x, y) = \frac{x}{y} \cdot a \cdot (1 - y) k$$

- The trait x is the level of competitiveness (or fighting effort).
- x/y is the competitive advantage to a focal individual.
- a is the amount of available resources per capita.
- $(1 - y)$ measures the extent to which competition between individuals destroys resources at the population level.

⁸The parameter $k = k(y)$ depends on the trait in the resident population and takes density-dependent competition into account.

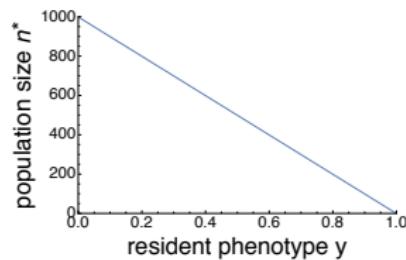
Explicit density-density dependence: Beverton-Holt model

We assume that population dynamics follows a Beverton-Holt with regulating factor

$$k = \frac{1}{1 + \gamma n^*}$$

This implies that for a resident population, the equilibrium population size is⁹

$$n^* = \frac{a \cdot (1 - y) - 1}{\gamma}$$



The equilibrium population size n^* is decreasing with y , and eventually takes a value of zero (basically as $y = 1$ if a is large).

⁹Obtained by setting $w(y, y) = 1$ and solving for n^*

Exploitation competition: the selection gradient

The selection gradient on the level of competition is

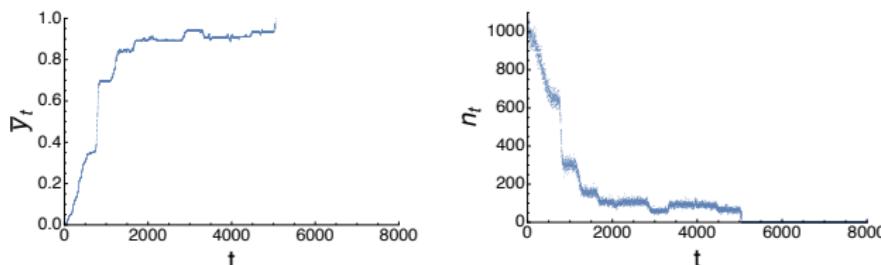
$$S(y) = a \frac{(1-y)}{y} k \geq 0$$

- The level of competitiveness is selected to increase at all trait values, since the right-hand side is always positive. We have **constant directional selection**.
- This is so because an individual always obtains a relative advantage by increasing the level of competition.
- The level of competition will eventually reach the value of one, but at this point the population will go extinct.

$S(y) > 0$ for all y \Rightarrow y increases \Rightarrow $n^* \rightarrow 0$

Selection driven evolutionary suicide

Running individual-based simulations produces



Parameters are $a = 1000$, $\gamma = 1$, $\bar{y}_0 = 0$, $n_0 \approx 1000$, $\mu = 10^{-3}$ (mutation rate) and $\sigma_\mu = 0.05$ (mutation step-size standard deviation).

- Asymptotic values are those predicted by the model: $y^* \rightarrow 1$ and $n \rightarrow 0$.
- The population goes extinct by evolution! This is called **evolutionary suicide**.

Good example of situations where there is an externality

Take home message one

- Small mutational phenotypic step size results in **adaptive sweeps** under broad conditions. Improvements are often small.
- By gradual change under long term-evolution a population evolves under two modes of selection:
 - ① Stabilizing selection. Here the population evolves towards **convergence stable strategies** that are locally **uninvadable**.
 - ② Disruptive selection (or diversifying selection). **Fitness landscapes are not static but dynamic.**

Take home message two

Two main modes of competition.

- ① Exploitation competition can result in **evolutionary branching** when there is limiting similarity and thus diversification. In a sense, natural selection is here “constructive”.

- ② Interference competition can result in **evolutionary suicide**. In a sense, natural selection is here “destructive”.

This is true for all competitive systems. Good examples of destructive components of competitive economic systems are their **externalities**.