When does evolution Optimise?

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Observations:
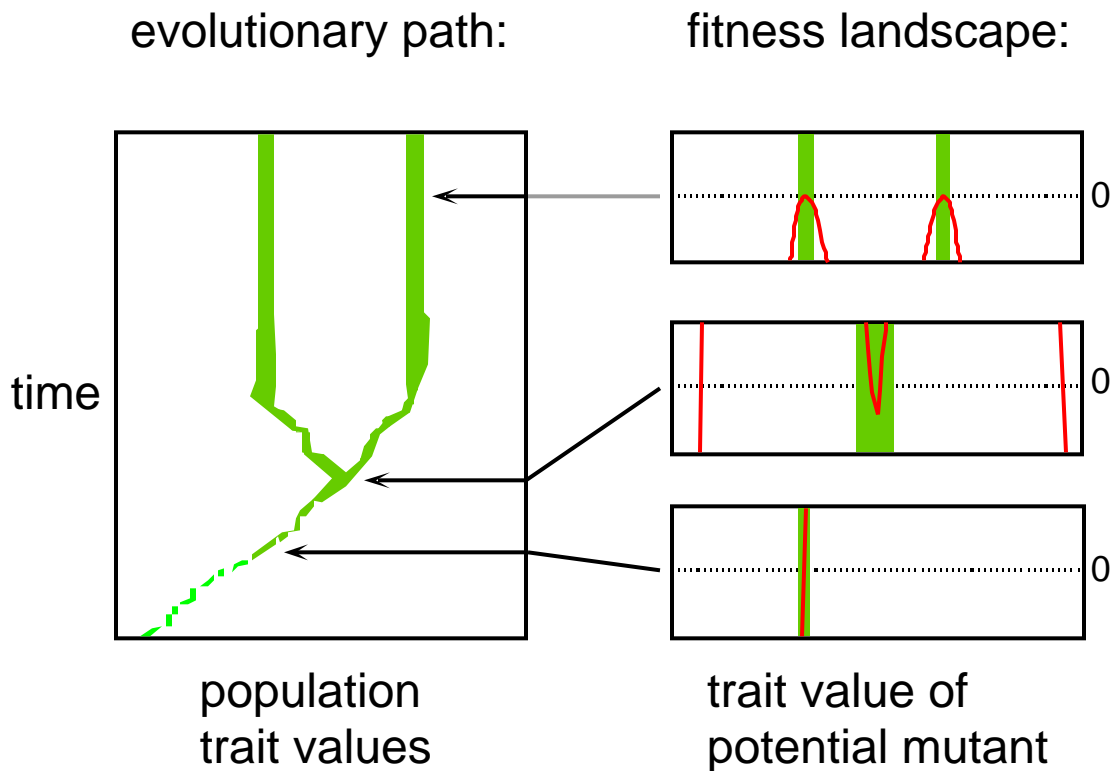
1.   Biological theorising is often done in terms of   optimisation models

2.   The quantity optimised customarily is supposed to be a "fitness measure"

3.   Two commonly used demographically based fitness measures are

the intrinsic rate of natural increase   r,
and
the mean lifetime offspring production R_0

(usually, but mistakenly, called basic reproductive rate as it is not a rate but a ratio)

4.   Some others are

the rate of energy gain
and
the carrying-capacity K

However, ...

PROBLEM WITH OPTIMISATION:

implicit assumption that
the fitness landscape is constant

no diversification !

evolutionary path: fitness landscape:

time

population
trait values

trait value of
potential mutant
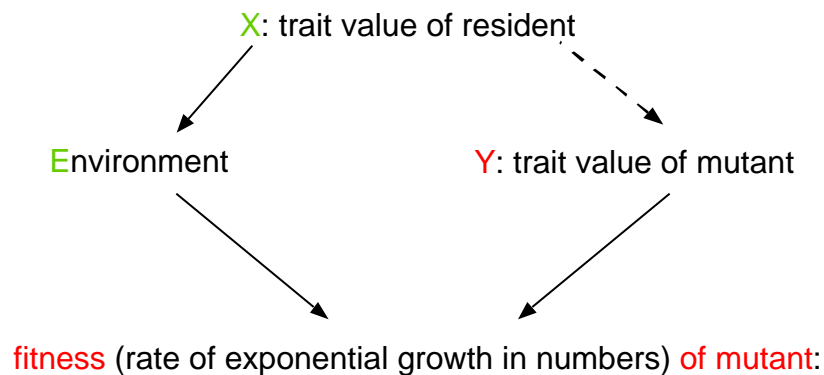
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Questions:

1. Under what conditions can evolution be conceived as optimising?

2. What does the optimisation principle look like in each case?

3. In particular, when is the quantity to be optimised r or $R0$?

4. Does all this attention to logical rigor make a difference?

Setting the stage: the steps of evolution

X: trait value of resident

Environment   Y: trait value of mutant

fitness (rate of exponential growth in numbers) of mutant:

$$(Y, E_{attr}(X)) =: s_X(Y)$$

* Y has a positive probability to invade into an X community
if and only if $s_X(Y) > 0$.

Convention:

Whenever I say / write
$$\text{"all E"}$$
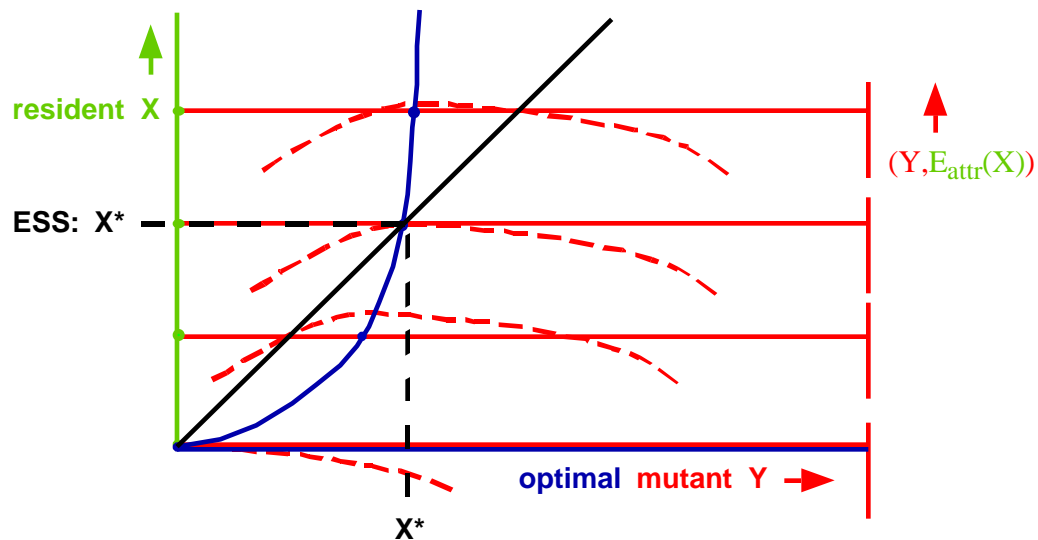I mean
$$\text{"all } E \text{ that can occur as } E_{Attr}(X) \text{ for some } X\text{"}.$$

ESS argument:

(1) Calculate for each $E_{attr}(X)$ the fitness $(Y, E_{attr}(X))$ for all potential trait values Y.

(2) Determine for each trait value the mutant which maximises $(Y, E_{attr}(X))$. The result is a function $Y_{opt}(X)$.

(3) Vary X to find an evolutionarily unbeatable value X*, i.e., an X* such that

$$Y_{opt}(X^*) = X^*.$$

resident X

ESS: X*

$(Y, E_{attr}(X))$

optimal mutant Y ➔

X*

(4) Ascertain that the set of trait values X_0 from which X* is approximated with non-zero probability through a sequence $X_0, X_1, X_2, \ldots$, such that

$$(X_{i+1}, E_{attr}(X_i)) > 0,$$

is sufficiently large to warrant consideration of X* as a potential evolutionary trap.

resident X

ESS: X*

$s_X(Y)$

optimal mutant Y

X*

y

−

+

+

−

x*

X
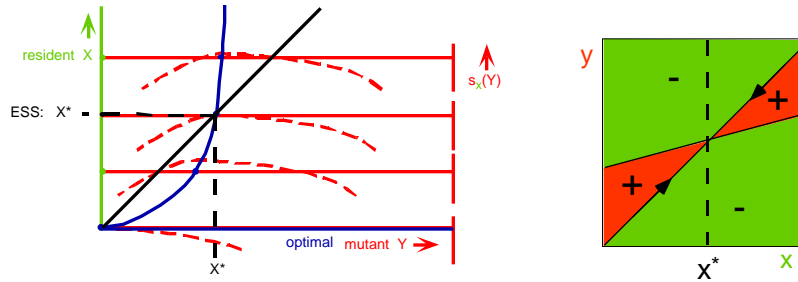
Remarks:

(i) For the first type of ESS calculation we may replace $s_X(Y)$ by any function, say $f(X,Y)$, such that for each X

$$f(X,Y) \quad \text{and} \quad s_X(Y)$$

are monotonically related as functions of Y.

(ii) For all ESS calculations we may replace $s_X(Y)$ by any function, say $g(X,Y)$, such that

$$\text{sign } s_X(Y) \;=\; \text{sign } g(X,Y)$$

(iii) When the community dynamics always has a global point attractor

$$\text{sign } \ln(R_0(E_{attr}(X),Y) \;=\; \text{sign } s_X(Y)$$

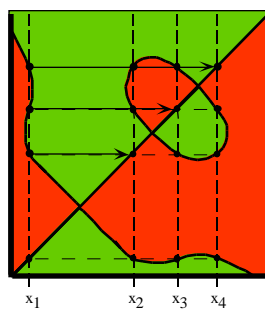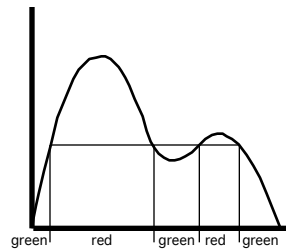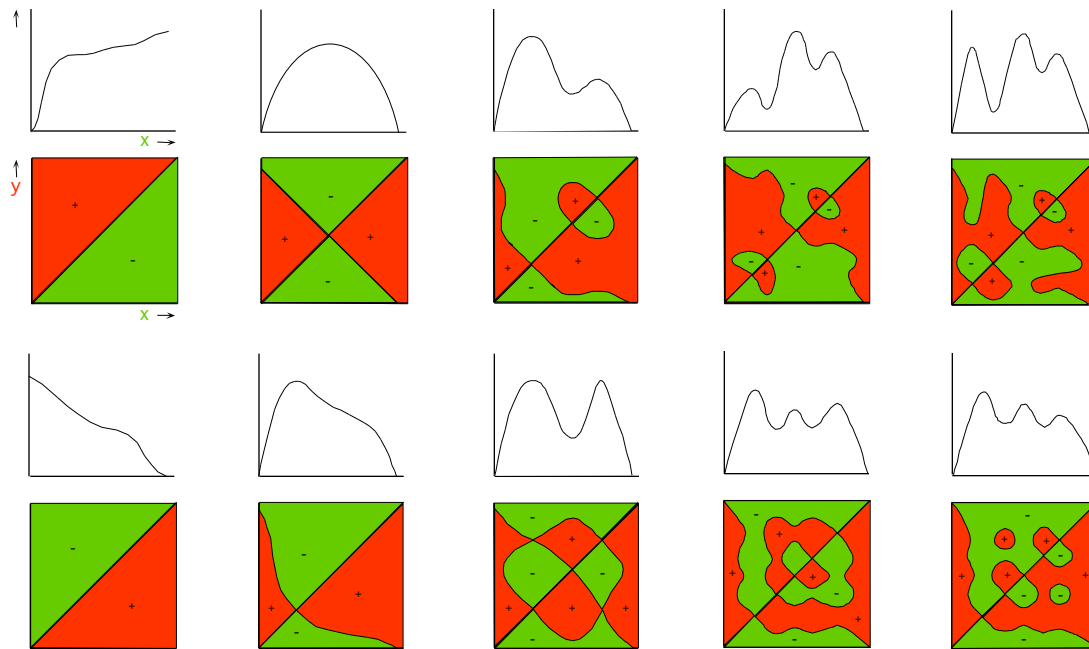
Questions:

1. Under what conditions can evolution be conceived as optimising?

2. What does the optimisation principle look like in each case?

3. In particular, when is the quantity to be optimised r or R_0?

4. Does all this attention to logical rigor make a difference?

Definition:

*   We shall call a function   of X to the real numbers with the property that evolution maximises **for any constraint on X** an

optimisation principle.

Some sign structures of $\rho(y, E_{attr}(x))$ that support an optimisation principle:

Convergence:

An Optimisation Principle
is
a Lyapunov function for the substitution proces

But

a Lyapunov function   for the substitution proces
is not necessarily
an optimisation principle.

Optimisation Principles are derived as properties of
families of models:
ecology plus trait space
plus all possible constraints on the trait space

Lyapunov functions are properties of a single model:
ecology plus trait space.

Questions:

1. Under what conditions can evolution be conceived as optimising?

→ 2. What does the optimisation principle look like in each case?

3. In particular, when is the quantity to be optimised r or R_0?

4. Does all this attention to logical rigor make a difference?

(i)

"Being more "efficient" increases your fitness
in any relevant environment."

(ii)

"Evolution minimises the availability
of a **limiting** resource"

Definition:

*   We shall call a function   of X to the real numbers with the property
that evolution maximises   for any constraint on X an

         optimisation principle.

•   And we shall call a function   of E to the real numbers with the property
that evolution minimises $(E_{attr}(X))$ for any constraint on X, a

         pessimisation or *Verelendungs principle*.

Let (X) be a prospective optimisation principle:

Then we expect by analogy of (i) from the one but previous slide that   can be written as

$$(X,E) = ((X),E),$$

with   increasing in its first argument, i.e.   .

The knowledge that only the sign of   matters lets us modify this to

$$\operatorname{sign} (X,E) = \operatorname{sign} ((X),E).$$

Definition:

* We shall say that

the trait vector acts
effectively one-dimensionally & monotonically

whenever there exists a function   of X to the real numbers such that

sign   (X,E) = sign   ((X),E),

for some function   which increasse in its first argument.

* We shall say that

the environment acts
effectively one-dimensionally & monotonically

whenever there exists a function   of E t o the real numbers such that

sign   (X,E) = sign   (X,   (E)),

for some function   which increases in its second argument.

Example:

Assume *that we only need to deal with constant environments, i.e., the community can alsways be assumed to be in a population dynamical equilibrium*

Whenever

(*) $R_0(X,E) =$ (E)$R_0(X,E_v)$,   "V" for "virgin",

Take

:= $\ln[R_0]$,   := $\ln[R_0]$,   := $R_0(X,E_v)$,

with R0 the so-called

basic reproduction ratio,

i.e., the lifetime production off offspring.

[(*) applies i.a. when the trait and the negative effect of the environment act in different life stages.]

Re the concept of "effectively one-dimensionally & monotonically acting environment":

Any   such that

$$\text{sign}\ (X,E) = \text{sign}\ (X,\ (E)),$$

with   increasing in its second argument,

can be interpreted as a

measure of environmental quality,

as perceived through the physiology of our individuals.

Propositions:

1:   Models in which
the trait vector acts effectively one-dimensionally & monotonically
have an optimisation principle,
and vice versa.

2:   Models in which
the environment acts effectively one-dimensionally & monotonically
have an optimisation principle,
and vice versa.

3:   For any optimisation principle there exists
a matched pessimisation principle,   and vice versa.

Examples (from evolutionary epidemiology):

I: density of infectives   S: density of susceptibles

Population equations:

$$dI/dt = [\ S - \ - d(S,I)]\ I \qquad dS/dt = [b - d(S,I) - \ I]\ S$$

with $d(S,I) = d_0 + h(S,I)$ and either

(1) $h(S,I) = \ S,$ (2) $h(S,I) = \ S^2,$ (3) $h(S,I) = \ (S + I)$

[in all three models the attractor is always a stable point equilibrium]

R_0 of mutant in given (S,I) background: nature of feedback loop:

(1) $R(\ ,\ ;S,I) = \ S\big/[\ + d_0 + \ S]$ 1 dimensional, monotone

(2) $R(\ ,\ ;S,I) = \ S\big/[\ + d_0 + \ S^2]$ 1-dimensional, non-monotone

(3) $R(\ ,\ ;S,I) = \ S\big/[\ + d_0 + \ (S+I)]$ 2-dimensional

Optimisation principles:

To calculate the optimisation principle for **model (1)** use:

$$R(\ ,\ ;S,I) = \ S\big/[\ + d_0 + \ S]$$

$$S^* = (\ + d_0)\big/(\ - \ )$$

Pessimisation principle:

R increases in S,   therefore S^* is minimised

Optimisation principle:

Minimising S^* means minimising $(\ + d_0)\big/(\ - \ )$, i.e., maximising

$-(\ + d_0)\big/(\ - \ ),$ or $(\ - \ )\big/(\ + d_0),$ or $\cdots$

Technical check (i)

To judge the effective dimension / monotonicity of the feedback loop we should

compare over the different values of (,)

the dependence of $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ ))$ on (,)

locally around those (,) that make $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ )) = 1$.

To show that in **model (2)** the feedback loop is non-monotone we start from:

$$R(\ ,\ ;S,I) = S \Big/ [\ + d_0 +\ S^2], \qquad S^* = [\ - (\ ^2 - 4\ \ (\ + d_0))^{1/2}] \Big/ (2\ )$$

R depends on $E = (S,I)$, and therefore on (,), in a 1-dimensional manner (through S only).

The maximum of R as a function of S lies at $S^{max}(\ ,\ ) = [(\ + d_0)/\ ]^{1/2}$.

Let (,) $M := \{(\ ,\ )\ |\ S^{max}(\ ,\ ) = S^*(\ ,\ )\}$. Then $R(\ ,\ ;S^{max}(\ ,\ )) = 1$.

(M is a curve in the (,)-plane.)

For sign $\ln[R(\ ,\ ;S)]$ to be monotonically related to some (E)

this should be maximal at $S = S^{max}(\ ,\ )$.

As $S^{max}(\ ,\ )$ varies when (,) is varied, no single can do this job.

Let sign $\ln[R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ ))] = $ sign $g(\ ,\ ;\ (E))$ for some function from E to the real numbers and a function g (not necessarily monotone in).

Then curves $(S^*(\ ,\ ),I^*(\ ,\ )) =\ _0$, with $_0$ defined by $g(\ ,\ ;\ _0) = 0$ map into curves $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ )) = 1$.

} curves of constant
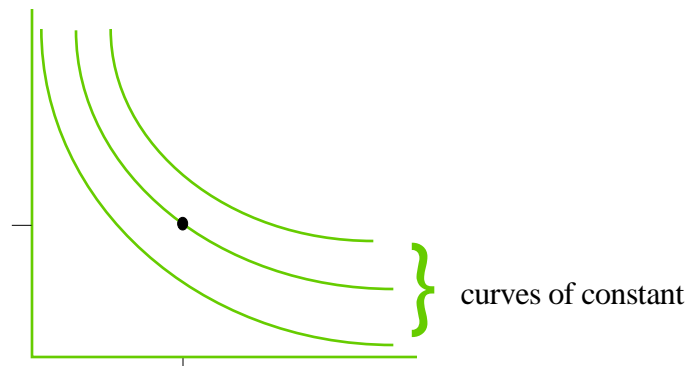
A curve through a point (,) = (,) should not change when we change (,) in such a manner that the resulting curves still pass through that point.

Technical check (ii)

To judge the effective dimension / monotonicity of the feedback loop we should
    compare over the different values of (,)
        the dependence of $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ ))$ on (,)
        locally around those (,) that make $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ )) = 1$.

To show that in **model (3)** the feedback loop is 2-dimensional we start from:

$$R(\ ,\ ;S,I) = \ S \big/ [\ + d_0 + \ (S+I)]$$

$$I^* = [(b-d_0)(\ -\ ) - \ - d_0] \big/ (\ ^2 - \ ^2 + \ ), \qquad S^* = (\ + d_0 + \ I^*) \big/ (\ -\ )$$

Define curves C(,) in (,)-space by $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ )) = 1$.
If the feedback loop were effectively 1-dimensional,   then for all (,)
the tangent at (,) = (,) to the curve $R(\ ,\ ;S^*(\ ,\ ),I^*(\ ,\ ))=1$ in (,)-space
should not vary when (,) moves over C.

   Manipulating partial derivatives shows that this is not the case.

On 1-dimensional but not necessarily monotonic E

conjecture: PIP is skew symmetric   (Stefan Geritz)

"proof": (a) ++ regions generically are excluded as generically
there cannot be an internal population dynamical equilibrium,
which should be there by Brouwer's fixed point theorem.
(b) -- regions are also generically excluded as for those
configurations there also should be an (unstable) fixed point:
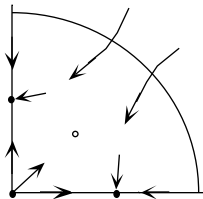
The two boundary fixed points have an open domain of attraction.
The complement the community state space is invariant.
Remove far away points and the neighbourhood of (0,0).
This gives an invariant closed set and therefore a fixed point
by Brouwer's theorem.

Skew symmetric PIP that allows Rock Scissors Paper behaviour
(Eva Kisdi):
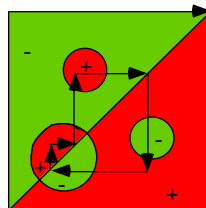
Questions:

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2. What does the optimisation principle look like in each case?

→ 3. In particular, when is the quantity to be optimised r or R_0?

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Assumption:

We only need to deal with
constant environments,
i.e., the community can always be assumed to be in
population dynamical equilibrium.

Proposition:

For constant environments

$$(X,E) = r(X,E).$$

Moreover,

$$r(X,E) \begin{array}{l} > 0 \\ = 0 \\ < 0 \end{array} \quad \text{if and only if} \quad R_0(X,E) \begin{array}{l} > 1 \\ = 1 \\ < 1, \end{array}$$

allowing the replacement of   in the ESS recipe by $\ln[R_0]$.

Definition:

We shall say that

*evolution **just** maximises* r, or R_0,

whenever

$$r(X,E_0), \quad \text{respectively} \quad R_0(X,E_0),$$

is an optimisation principle **for every choice of E_0.**

Proposition:

Evolution just maximises r, or R_0,

if and only if

it deals with a combination of life histories and
ecological embedding such that is possible to write

$$r(X,E) \ = \ \quad (r(X,\ E_0),X),$$

or

$$R_0(X,E) \ = \ \exp[\ \quad (\ln[R_0\ (X,\ E_0)],X)],$$

respectively,

with   increasing in its first argument,
and E_0 fixed, but otherwise arbitrary.

Examples:

1: Whenever the environment makes itself felt only through an additional death rate $\mu(E)$,
   acting equally on all individuals, r(X,E) can be expressed as

$$r(X,E) = r(X,E_V)- \mu(E),$$

E_V the virgin environment. Therefore evolution within those confines just maximises r.

2: Whenever the trait and the environment affect non-overlapping life stages,
   $R_0(X,E)$ can be expressed as

$$R_0\ (X,E) = \quad (E)R_0\ (X,E_V),$$

E_V the virgin environment. Therefore evolution within those confines just maximises R_0.

Questions:

   1. Under what conditions can evolution be conceived as optimising?

   2. What does the optimisation principle look like in each case?

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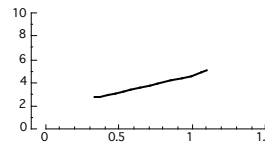➤   4. Does all this attention to logical rigor make a difference?

Example:
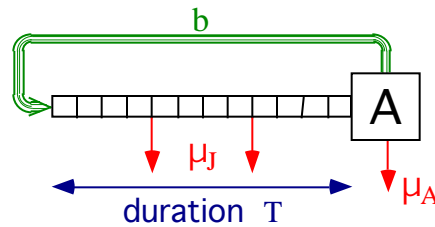
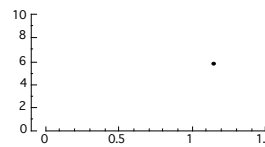|	In general:	In the Virgin environment:
Length of juvenile period	$T(T_V, E)$	T_V
Juvenile death rate	$\mu_J(E)$	μ_{JV}
Adult death rate	$\mu_A(E)$	μ_{AV}
Birth rate (to adults)	$b(T_V, E)$	$b_V(T_V) = (T_V - 1)_+$

1. E **only** equally additively affects the juvenile and adult mortality rates
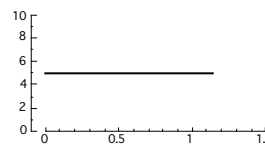
    maximise r

2. E **only** additively affects the adult mortality rate
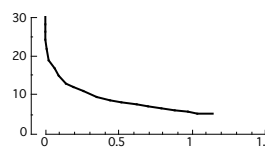
    maximise R_0

3. E **only** multiplicatively affects the reproduction rate

    maximise R_0

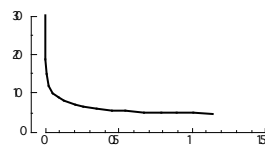4. E **only** additively affects the age at maturation (*but not the birth rate*)

    maximise R_0

5. E **only** multiplicatively affects the age at maturation (*but not the birth rate*)
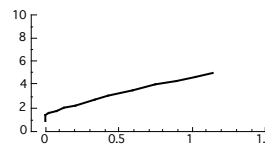
    maximise

    $T_V^{-1}[ln(b_V(T_V)) - ln(\mu_{AV})]$

6. E **only** additively affects the juvenile mortality rate:

    maximise

    $T_V^{-1}[ln(b_V(T_V)) - ln(\mu_{AV})]$

Length of juvenile period T^* in the field

Field adult mortality μ_A