FdV Jan 2013

The Interaction Between Evolution and Ecology

Part 2!

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Original Proposition

- Introduction into Adaptive Dynamics
- Application: Virulence Evolution
- Application: Kin Selection, Cooperation, and Units of Adaptation

Potential Topics

Synthetic Biology, Experimental Evolution

Mechanisms and Evolutionary Outcomes

Invasion Biology & Evolution

Genomics & Information Theory

Invasion

Evolution and Ecology

- Population Genetics
- Game Theory
- Life History Theory
- Community Ecology

Population Genetics

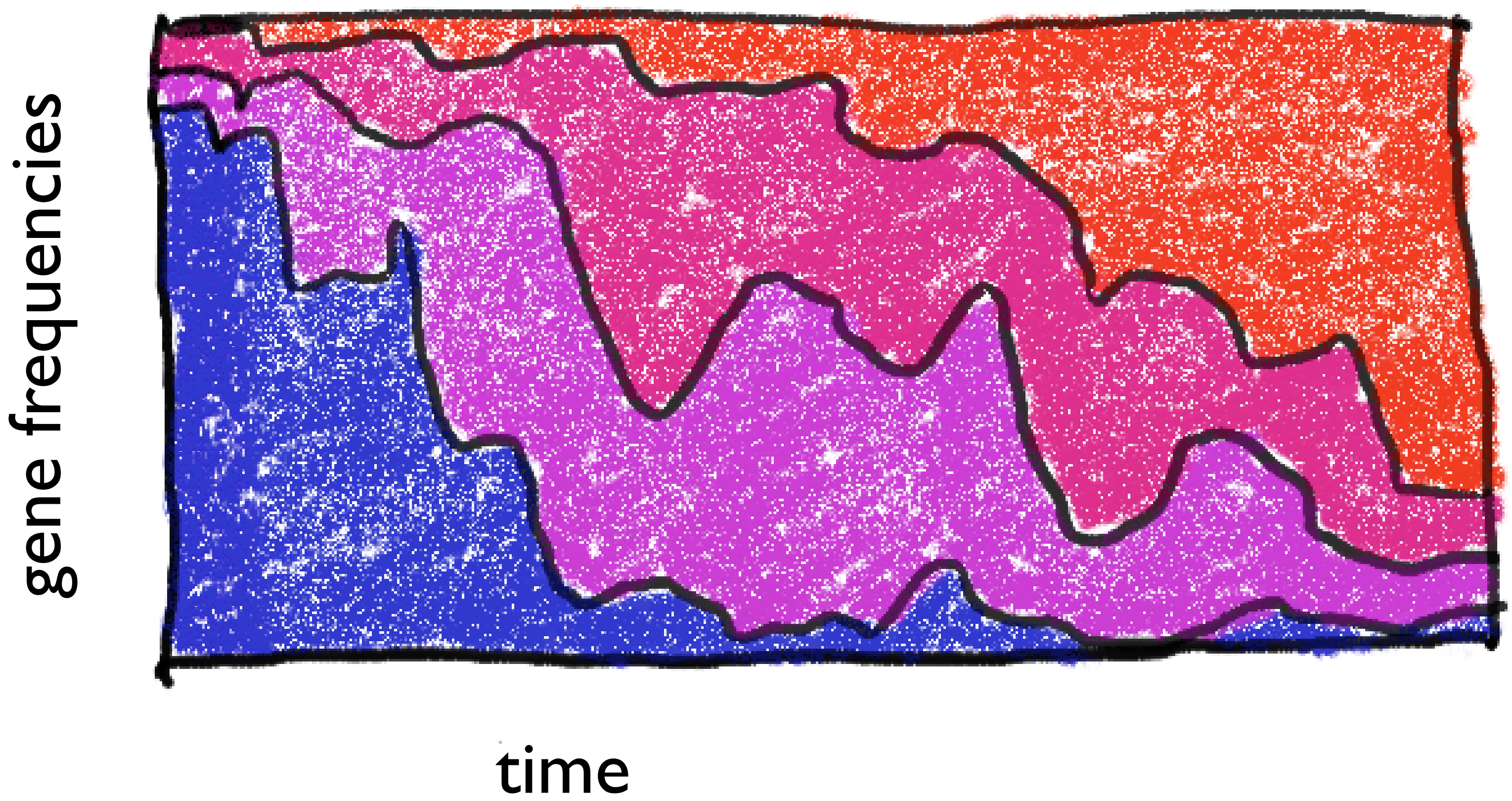
Population Genetics

Well-known standard case:

- Sexual reproduction
- Diploid genetics
- Two alleles (dominant/recessive)

Variables: gene frequencies

Gene frequencies



Population Genetics

Typical assumptions:

- single population
- simplified ecology
  - most ecological aspects are subsumed in 'frequency dependence'
- more realistic cases difficult to analyse
  - density dependence
  - population interactions

$$\frac{dx_i}{dt} = (b_i - d_i)\, x_i$$

$$= r_i x$$

maybe density dependent!

$$r_i = f_i(\ldots, x_j, \ldots)$$

$$i = a, A$$

$$p_a = \frac{x_a}{x_a + x_A}$$

$$\frac{dp_a}{dt} = \frac{\frac{dx_a}{dt}(\cancel{x_a} + x_A) - x_a\left(\cancel{\frac{dx_a}{dt}} + \frac{dx_A}{dt}\right)}{(x_a + x_A)^2}$$

$$= \frac{\frac{dx_a}{dt} x_A - x_a \frac{dx_A}{dt}}{(x_a + x_A)^2}$$

$$= \frac{r_a x_a x_A - r_A x_A x_a}{(x_a + x_A)^2}$$

$$= \frac{x_a x_A}{(x_a + x_A)^2}(r_a - r_A)$$

$$= p_a(1 - p_a)(r_a - r_A)$$

<u>if</u> $r_a = r_A(1+s)$

then $\frac{dp_a}{dt} = p_a(1-p_a)r_A s$ ← "selection coefficient"

Measures of increase

Subtle differences

- λ rate of population increase
  - invasion continuous time : $\lambda > 0$
  - invasion discrete time : $\lambda > 1$
- R_0 basic reproduction ratio of individuals
  - invasion : $R_0 > 1$
- r net rate of reproduction of population
  - invasion : $r > 0$
- s selection coefficient
  - increase in frequency : $s > 0$

Population Genetics

Much attention to

- interaction among alleles and loci
  - dominance
  - modifiers
  - conditions that favour polymorphism
  - epistasis, linkage
  - links with developmental biology

Population Genetics

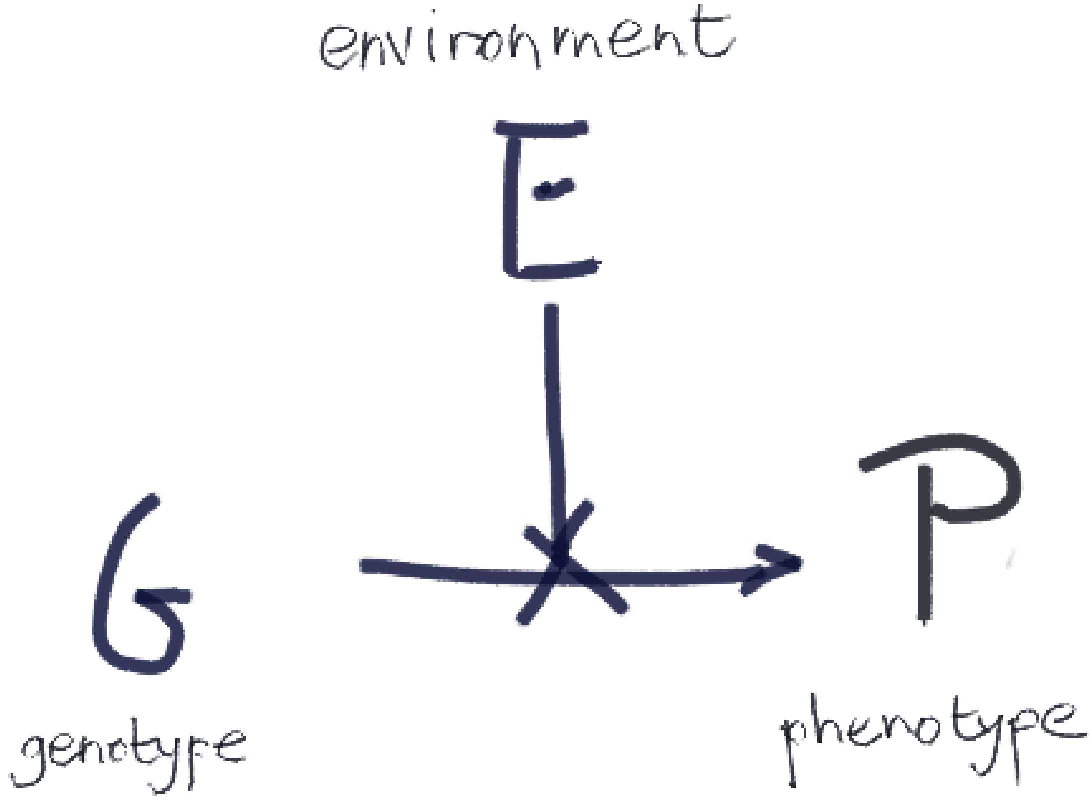
Little attention to

- Interactions among individuals
  - Population dynamics and ecology
  - Behaviour

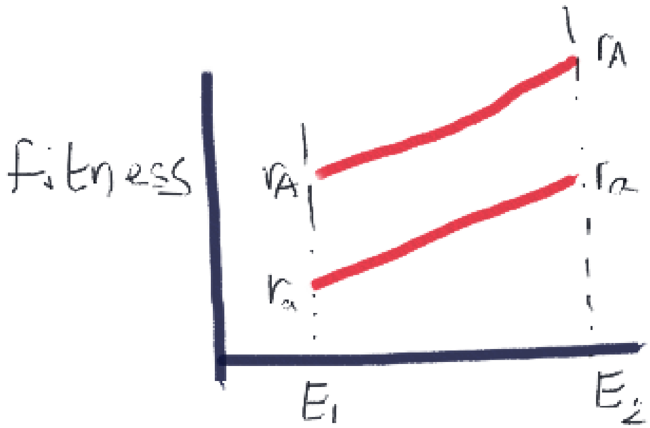
density dependence

phenotypic plasticity

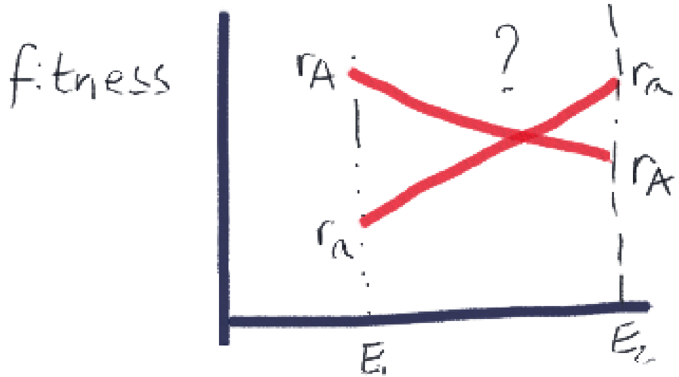
Phenotypic plasticity



Phenotypic plasticity

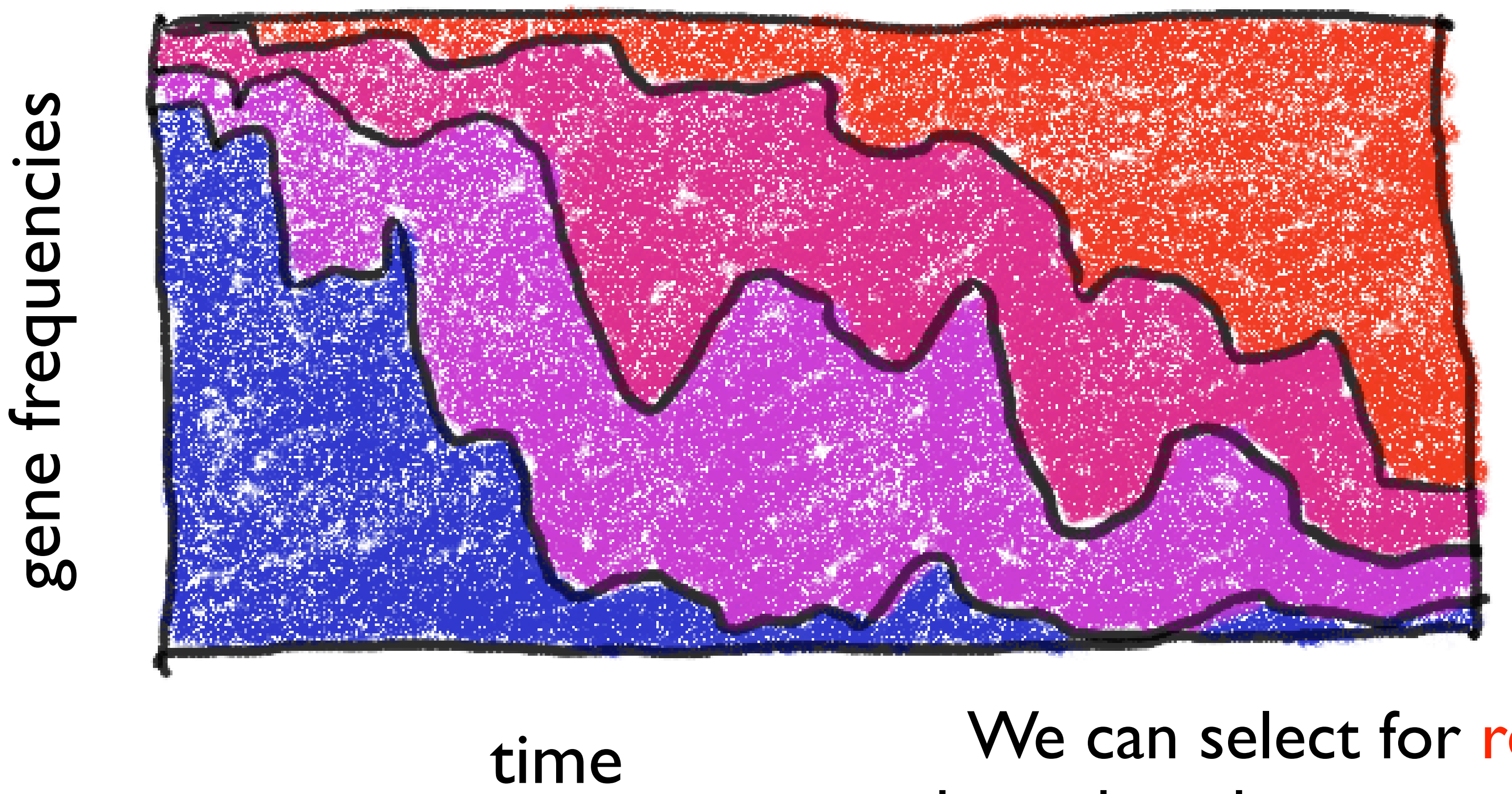


A dominates



it depends…

Gene frequencies



We can select for redness
but what about greenness???

Population Genetics

Caricature:

- ‘Evolution is change in gene frequencies’
- ‘That problem has been solved long ago’
- ‘The big problem is to explain speciation’

Game Theory

Game Theory

First developments during 2nd World War

Then applied to Sociology

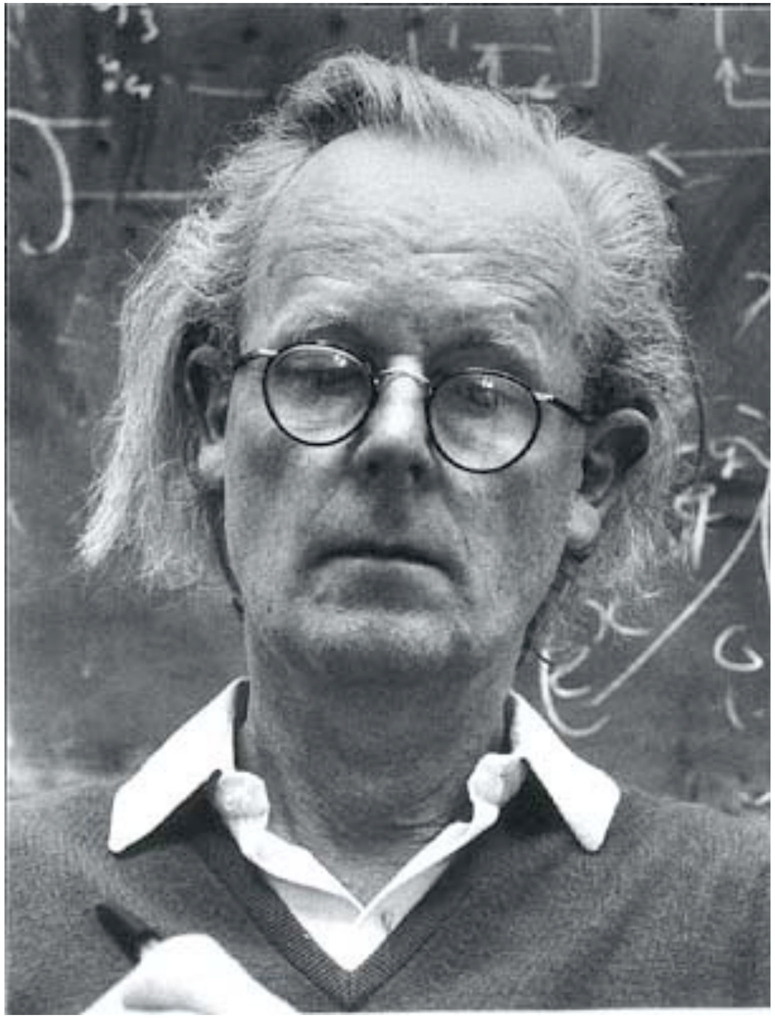
- Why do individuals cooperate?

Applied to Behavioural Ecology

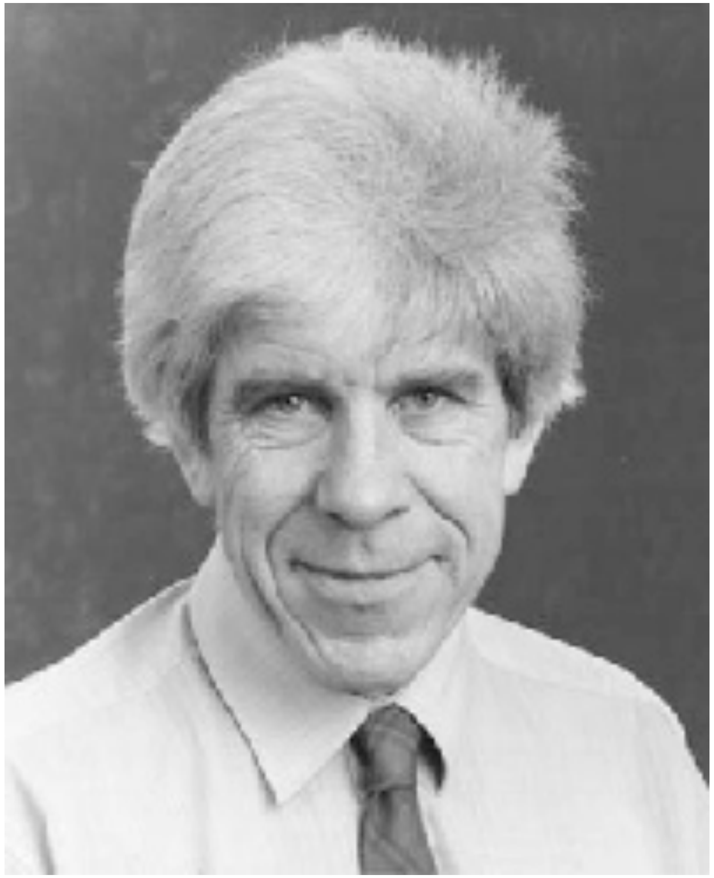
- Interactions among individuals

Bill Hamilton
John Maynard Smith

John Maynard Smith



Bill Hamilton



Evolutionary Game Theory

Observation: fighting animals rarely kill

Why such restraint?

Hawk-Dove Game

Maynard Smith & Price 1971

Game Theory

Individuals may choose among a range of strategies

Sometimes finding the optimum strategy is easy

Often, however, payoffs depend on what others do

The Hawk-Dove Game

		your opponent	
		H	D
you	H	$\frac{1}{2}(V-C)$	V
	D	0	$\frac{1}{2}V$

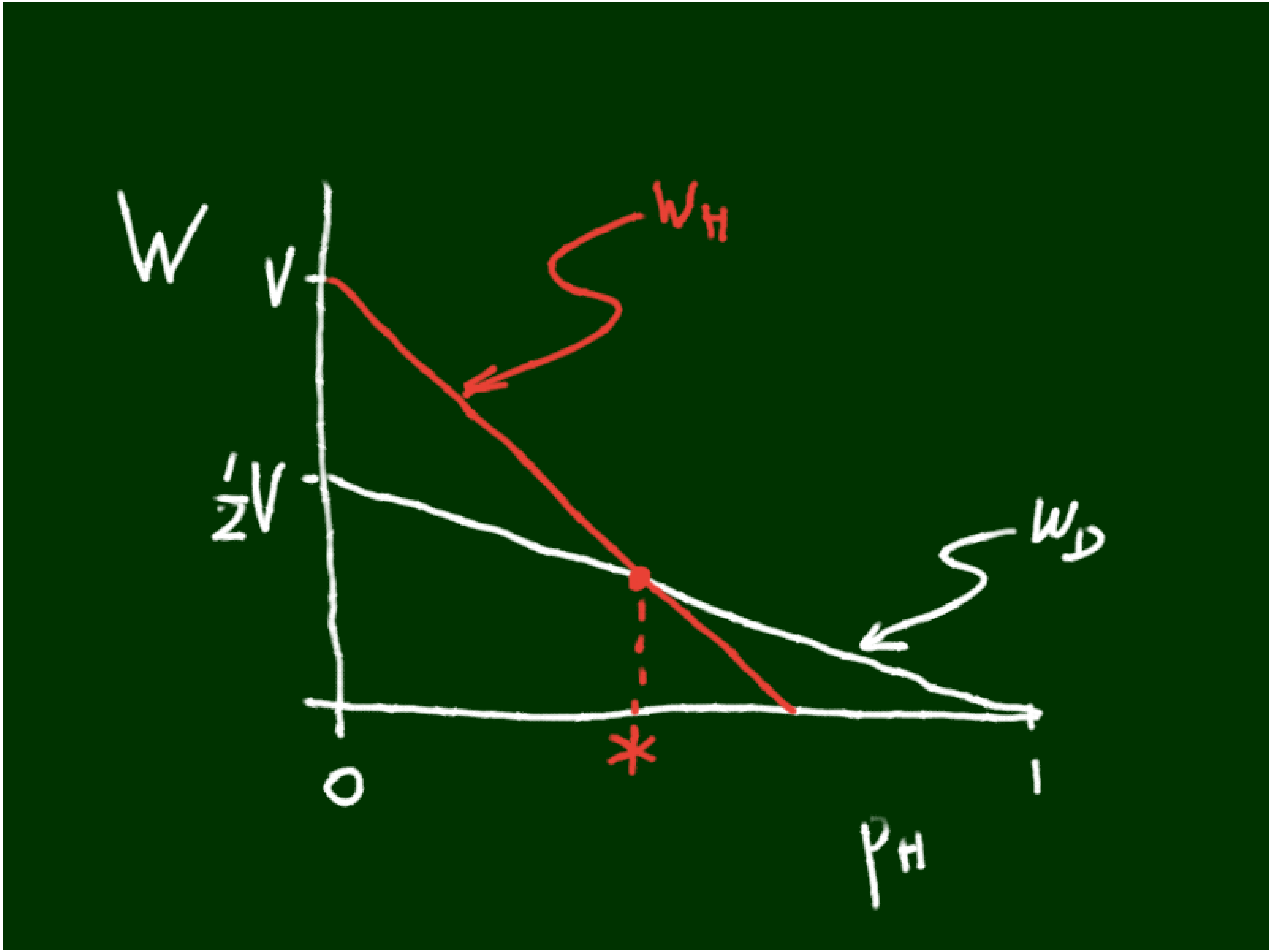
p_H : proportion Hawks

$$w_H = p_H \frac{1}{2}(V - C) + (1 - p_H)V$$

$$= V - \frac{1}{2}(V + C)\, p_H$$

$$w_D = p_H \cdot 0 + (1 - p_H)\frac{1}{2}V$$

$$= \frac{1}{2}V - \frac{1}{2}V p_H$$



W
V
½V
W_H
W_D
0
*
1
p_H

Evolutionarily Stable Strategies

If $p_H < p^*$ (few Hawks) then play 'Hawk'

If $p_H > p^*$ (many Hawks) then play 'Dove'

If $p_H = p^*$ both 'Hawk' and 'Dove' do equally well

A resident strategy that plays 'Hawk' with probability p^* cannot be beaten

Formalised in concept of ESS

John Maynard Smith,
Richard Dawkins

Evolutionary Stability

If for all strategies $J \neq I$

$$W(I|I) > W(J|I)$$

then strategy I is an ESS

~~If $W(I|I) = W(J|I)$ then I is ESS if $W(I|J) > W(J|J)$~~

- Maynard Smith & Price's second condition

convergence stability

Evolutionary Game Theory

Caricature:

- ‘The fitness of an individual depends
- on the strategies it adopts
- (which can be either pure or mixed)
- but also depends on the resident strategies
- according to the payoff function’

Evolutionary Game Theory

Problems

- where do the strategies come from?
  - Physiology?
  - Developmental genetics?
  - Behaviour?
  - Life History Theory?
- where does the payoff function come from?

Example: Sex Allocation

In many species, mothers can decide the sex of their offspring

- Strategy = {% sons, % daughters}

Fischer in the 30s:

- produce 50% daughters

Hamilton in the 60s:

- depends on mating structure
- biased sex ratios

Ex: Habitat Selection

In many spatially heterogeneous environments, individuals can decide
where to go

Often, payoffs depend on where others go

Q1: where should you go ?

Q2 (knowing A1) where does everybody go?

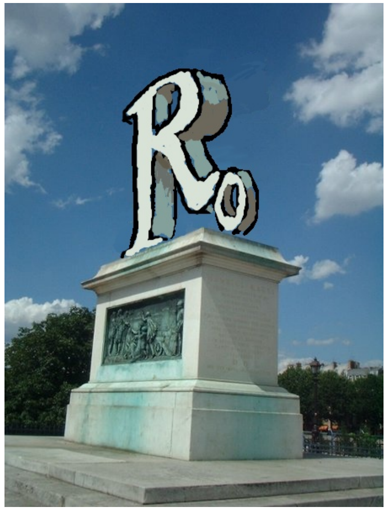
Prediction: Ideal Free Distribution

- nobody gains by moving to another place

Evolutionary Game Theory

Where does the payoff function come from?

- Fitness = Lifetime reproductive succces
- If Fitness > 1 ⇒ Invasion
- Life History Theory



Important Insights

Population Genetics

- mutant genotypes may generate new phenotypes

Game Theory

- outcome of interaction depends on conditions

Life History Theory

- rare mutants will try to optimize their strategies

Ecosystem Dynamics

- invasion of rare species, density dependence

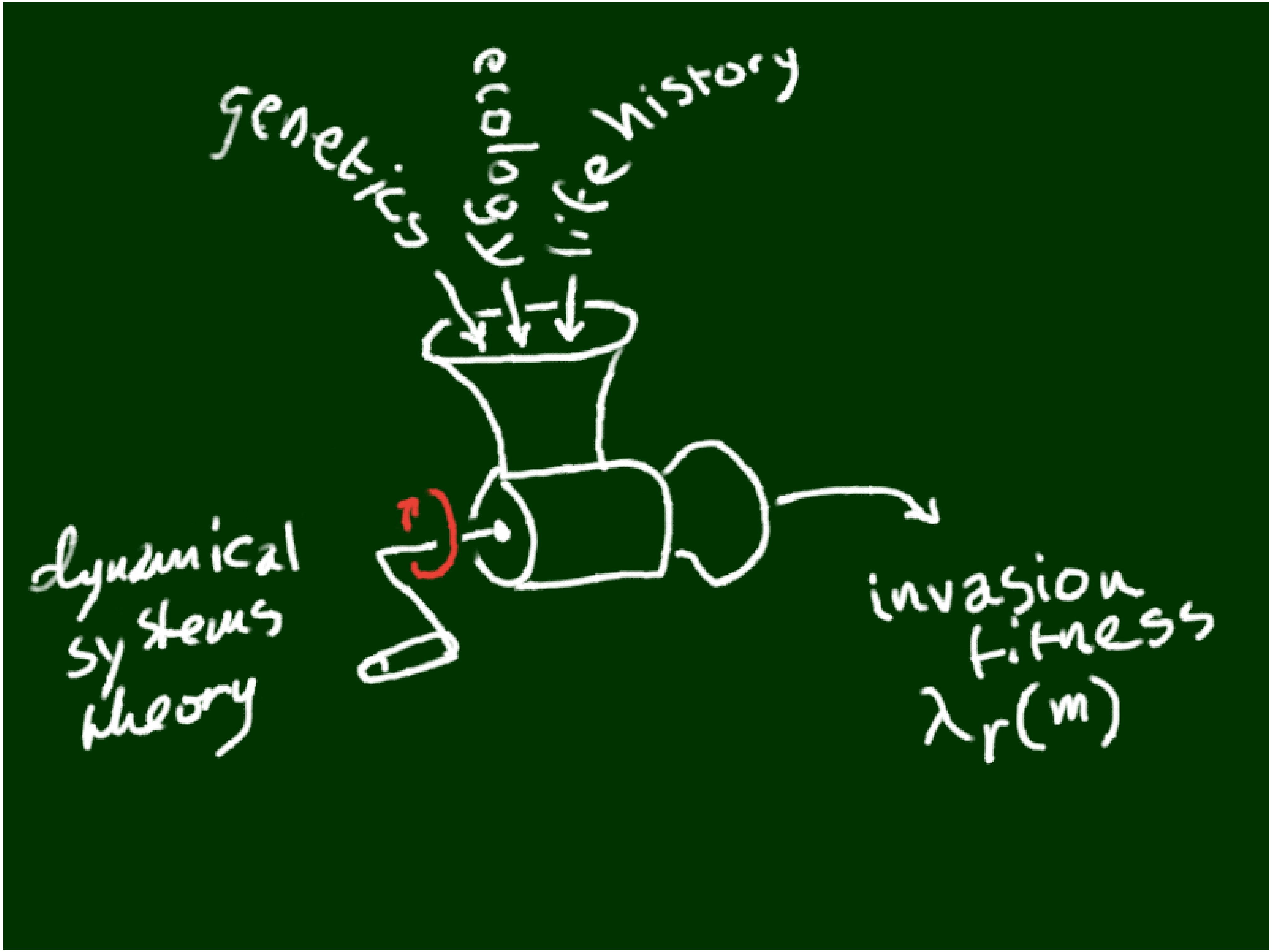
Adaptive Dynamics

Adaptive Dynamics

Caricature

- ‘New mutants may appear
- initially rare
- whose invasion fitness
- depends on the resident attractor’

Peter Hammerstein, Ilan Eshel, Hans Metz,
David Rand, Geza Meszena,
Ulf Dieckmann,
Stefan Geritz, Eva Kisdi.



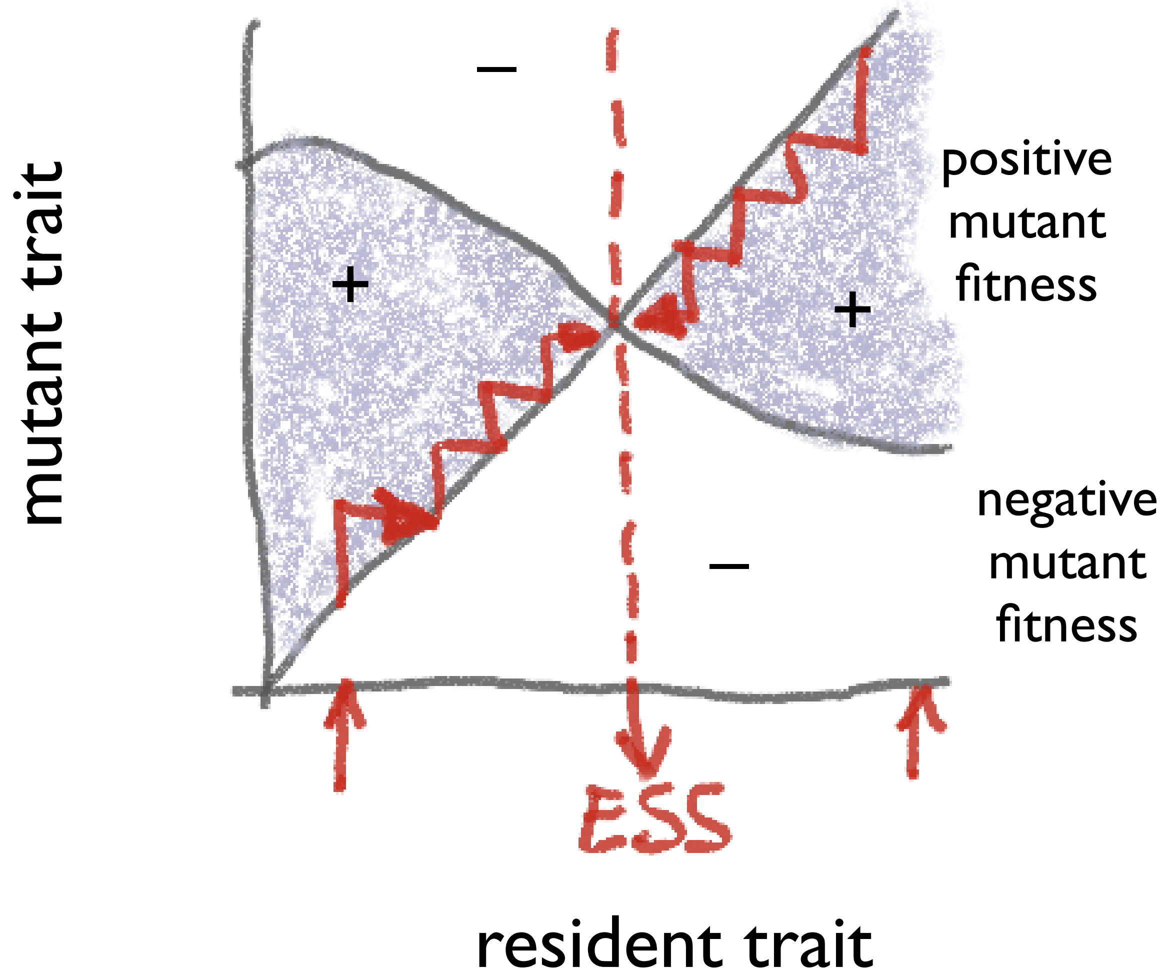
genetics
ecology
life history
dynamical systems theory
invasion fitness
$\lambda_r(m)$

Adaptive Dynamics

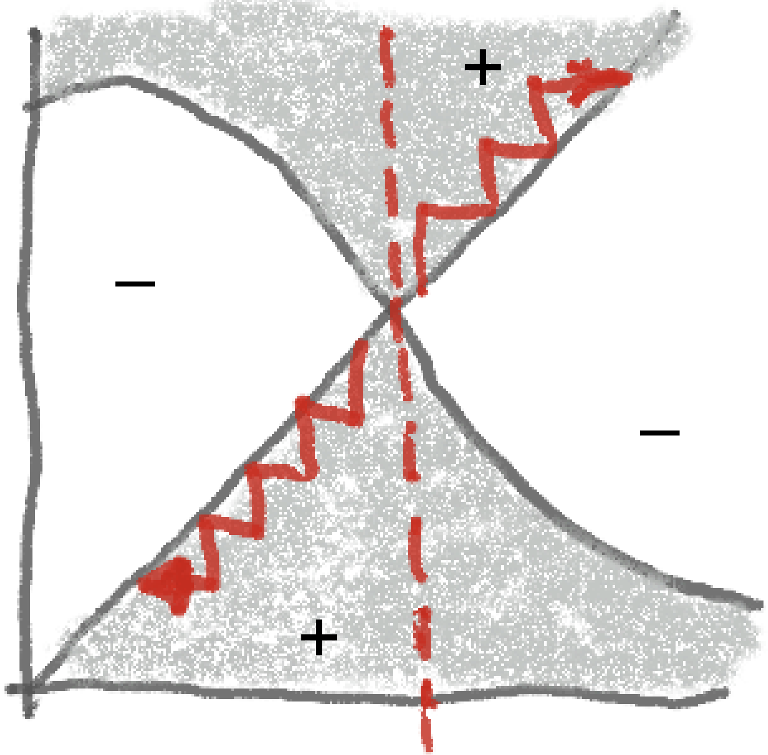
Practical Method

- monomorphic population trait a
- resident dynamics
- attractor
- mutant invasion
- pairwise invasibility plot (PIP)

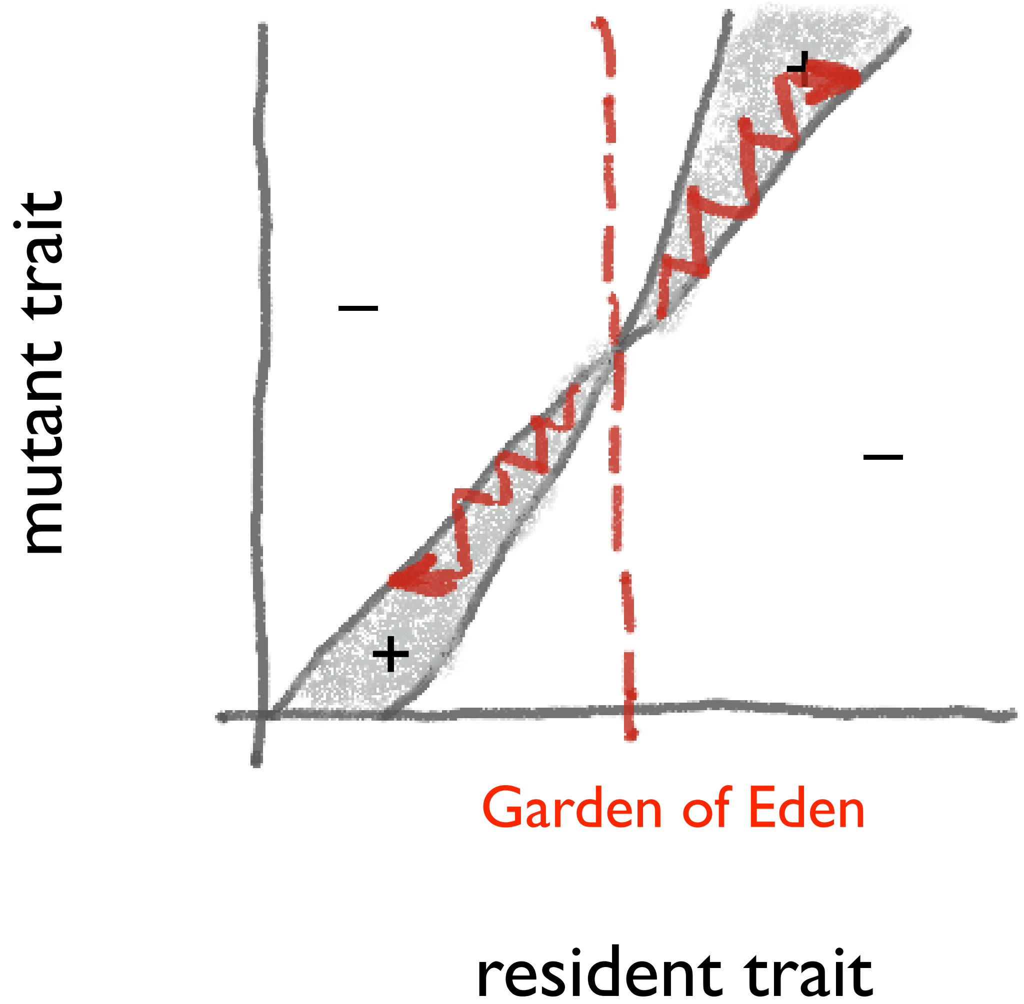
Pairwise Invasibility Plot



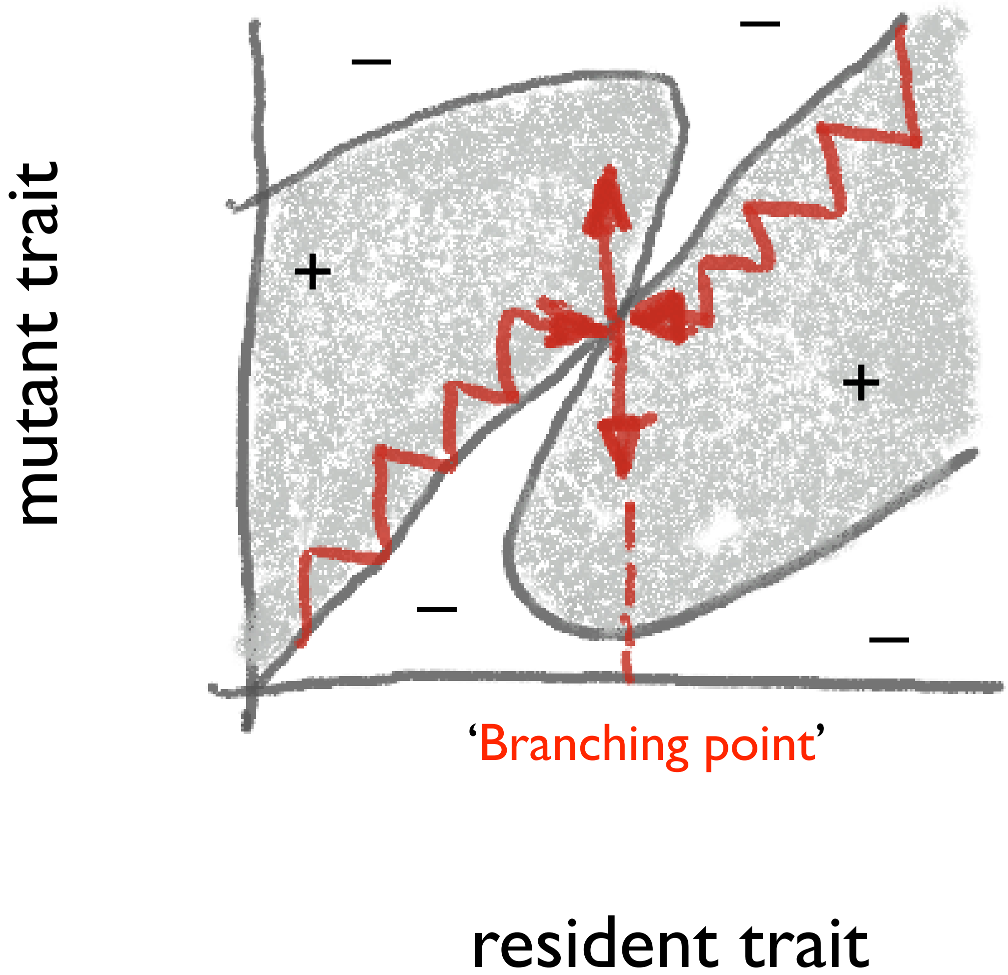
Pairwise Invasibility Plot



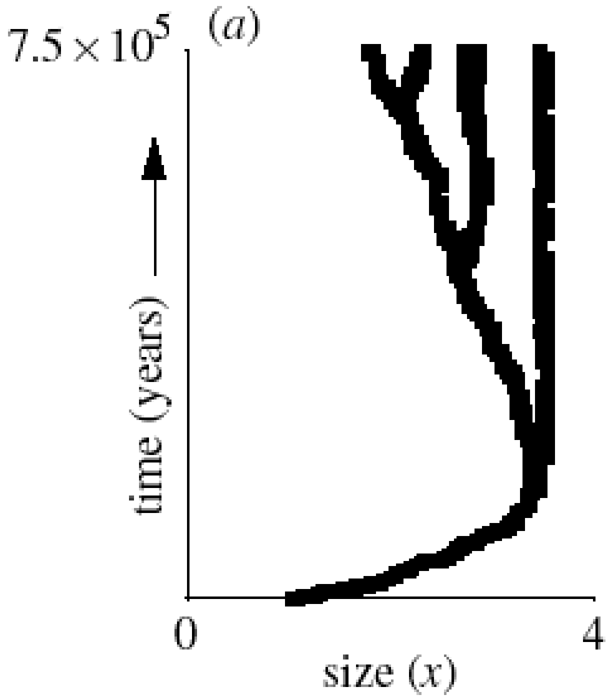
Pairwise Invasibility Plot



Pairwise Invasibility Plot



Kisdi & Geritz



Epidémiologie

$$\frac{dS}{dt} = [\text{host reproduction}] - \mu S - \beta SI$$
$$\frac{dI}{dt} = \beta SI - (\mu + \alpha) I$$

Individu
↓
Population

β paramètre de transmission
μ mortalité de base
α mortalité induite, virulence

Epidémiologie + Evolution

$$\frac{dS}{dt} = [\text{host reproduction}] - \mu S - \beta SI - \beta^* SJ$$

$$\frac{dI}{dt} = \beta SI - (\mu + \alpha) I$$

$$\frac{dJ}{dt} = \beta^* SJ - (\mu + \alpha^*) J$$

I souche residente, *J* souche mutante

« Dynamique adaptative »

- théorie des jeux dans un cadre écologique
- pour deriver la valeur sélective (fitness)
  - en lieu de simplement *supposer* l'expression
- pour predire la réponse evolutive
  - stratégies evolutivement stable
  - branchement évolutif

Articles par Metz, Kisdi, Geritz, Law, Rand, Dieckmann…

L'invasion des mutants

- Resident *I* en équilibre endemique

  $dI/dt = 0$

- Le mutant *J* envahit si

  $dJ/dt > 0$

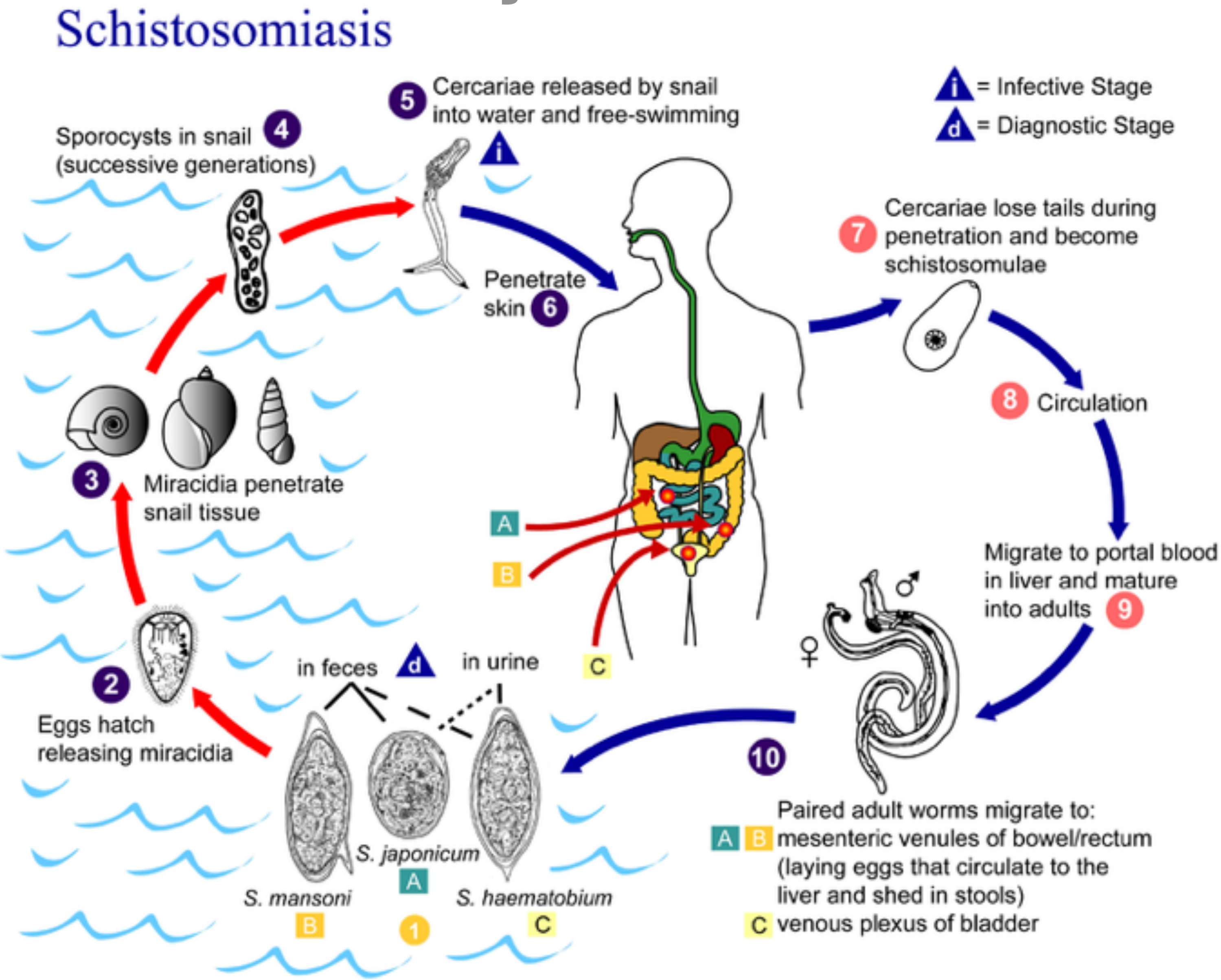
  (quand il est rare, $J << I$)

- Invasion si

$$\frac{\beta^* \bar{S}}{\mu + \alpha^*} > 1$$

R_0

R_0 easy to calculate?



Invasion

- Mutant *J* envahit si

$$\frac{\beta^* \bar{S}}{\mu + \alpha^*} > 1 = \frac{\beta \bar{S}}{\mu + \alpha}$$

$$\frac{\beta^*}{\mu + \alpha^*} > \frac{\beta}{\mu + \alpha}$$

La virulence optimale maximise $\frac{\beta^*}{\mu + \alpha^*}$

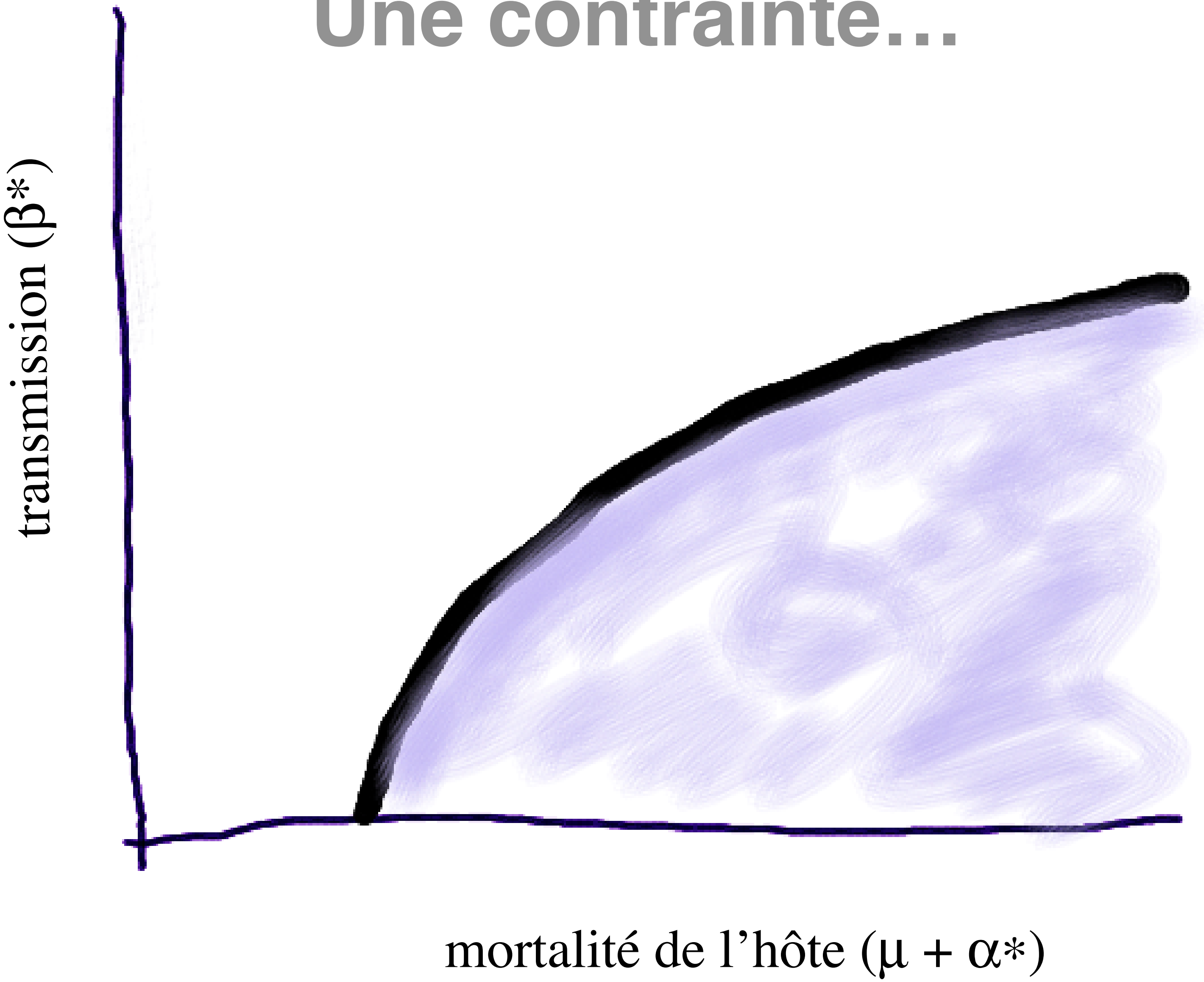
ESS

- La séléction naturelle favorise les parasites
  - qui maximisent

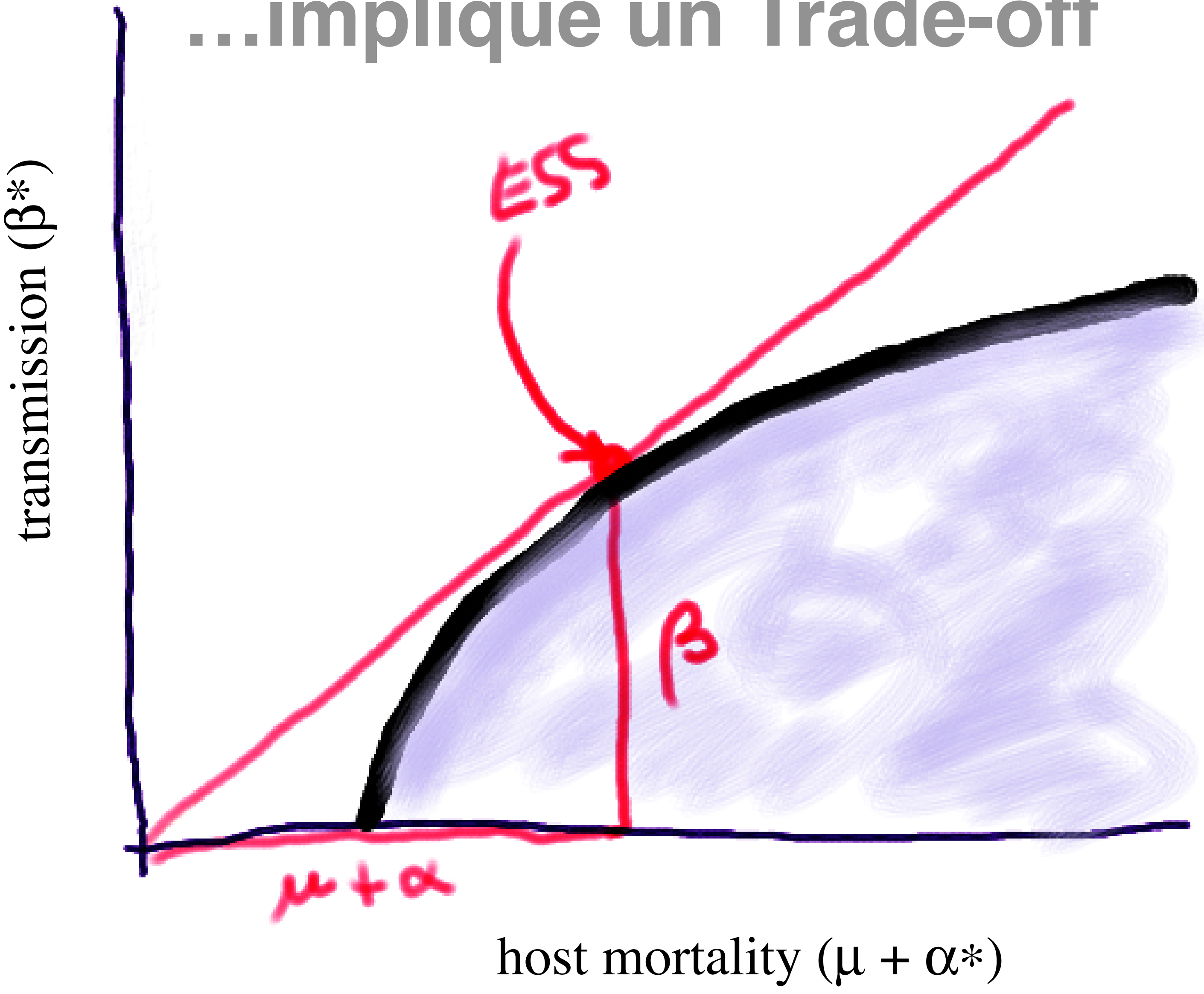
$$\frac{\beta^*}{\mu + \alpha^*}$$

  - exploitent leurs hôtes d'une façon optimale
    - les individus infectés, pas la population !

Une contrainte…



…implique un Trade-off



Epidémiologie + Evolution + Intervention

$$\frac{dS}{dt} = [\text{host repr.}] - \mu S - D\beta SI - D\beta^* SJ$$

$$\frac{dI}{dt} = D\beta SI - (\mu + \alpha) I$$

$$\frac{dJ}{dt} = D\beta^* SJ - (\mu + \alpha^*) J$$

I souche residente, *J* souche mutante

D modification de transmission

Invasion

- Mutant *J* envahit si

$$\frac{D\beta^*\bar{S}}{\mu+\alpha^*} > 1 = \frac{D\beta\bar{S}}{\mu+\alpha}$$

$$\frac{\beta^*}{\mu+\alpha^*} > \frac{\beta}{\mu+\alpha}$$

La virulence optimale maximise $\dfrac{\beta^*}{\mu+\alpha^*}$

Evolution

- Les parasites maximisent

$$\frac{\beta^*}{\mu + \alpha^*}$$

une quantité qui ne dépend pas de *D*!

Conséquences

- La virulence dépend de la forme du trade-off
  - la rélation entre transmission et mortalité
  - déterminée par la physiologie de l'hôte/ parasite
- La virulence ne dépend *pas* de facteurs externes
  + à l'exception du taux de mortalité de base
  - pas de rôle pour l'épidémiologie

Virulence Déterminée au…

niveau de la population

interactions sociales, interactions ecologiques, compétition, ressources, santé publique

niveau de l'individu

virulence

niveau intra-hôte

physiologie, dynamique intra-hôte, choses moleculaires, médicaments, antibiotiques

Conséquences

- Virulence depend de la forme du trade-off
  - + dépend de la physiologie de l'hôte
  - + dynamique intra-hôte du parasite
  - + système immunitaire
- – La virulence ne dépend *pas* de facteurs externes

Le dilemme du parasite

Le dilemme du parasite

- Un parasite peut
  - augmenter sa transmission, ou
  - prolonger la duration de l'infection
  - mais pas les deux en même temps
- ce dilemme est capturé par l'analyse graphique…

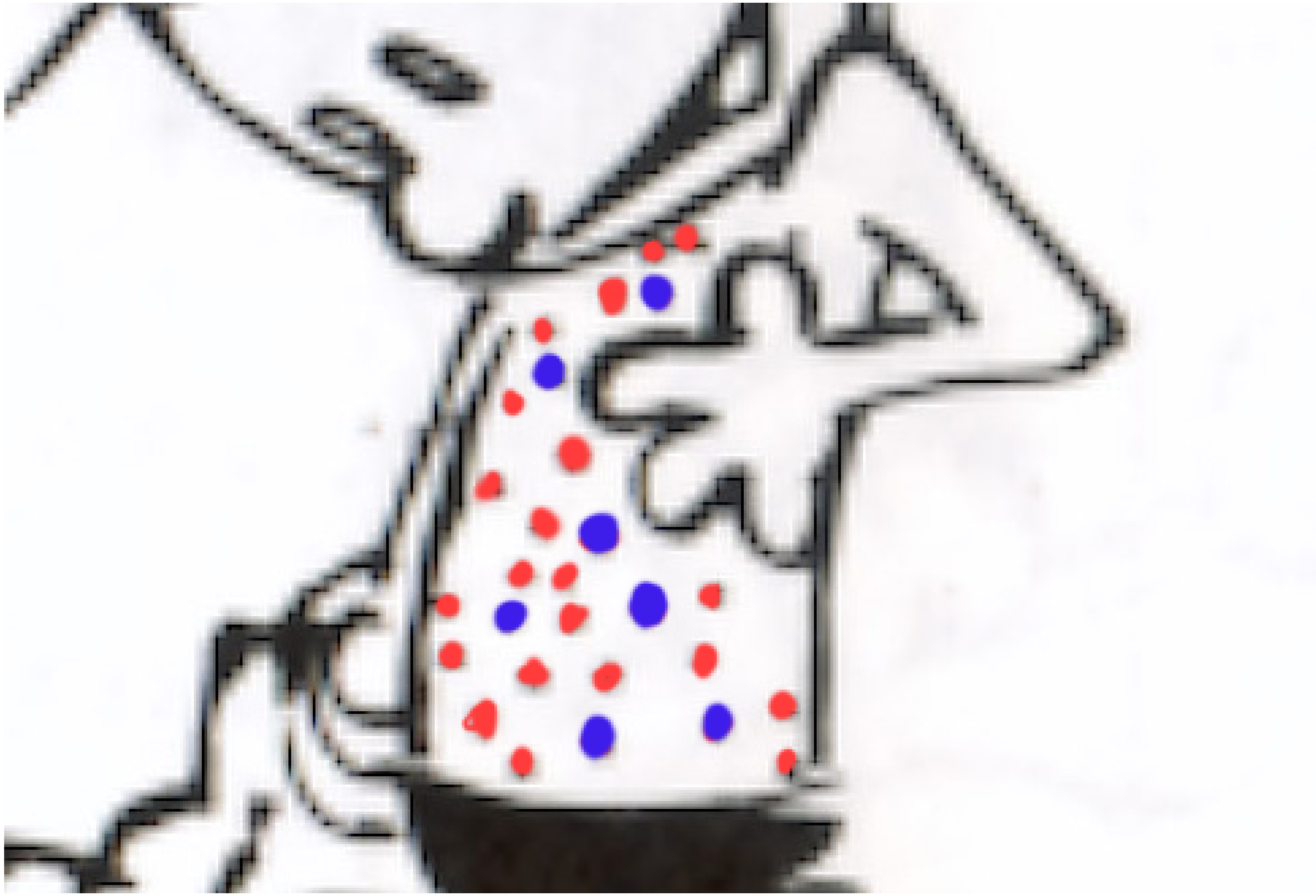
…mais… la réalité ?

- dans le modèle :

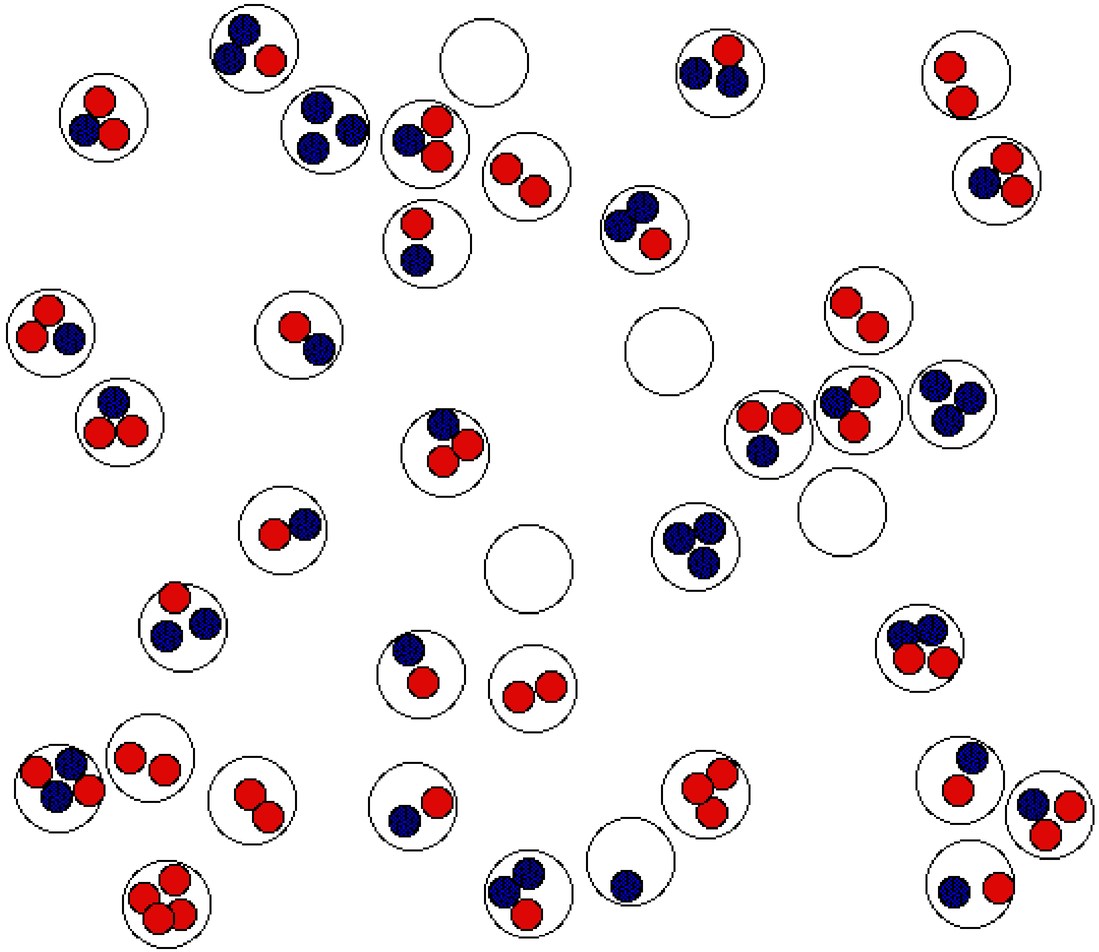
  durée de l'infection = survie de l'hôte

- souvent pas très réaliste :
  - infections terminées par le système immunitaire (guérison)
  - compétition avec d'autres parasites

Infections multiples



Infections multiples



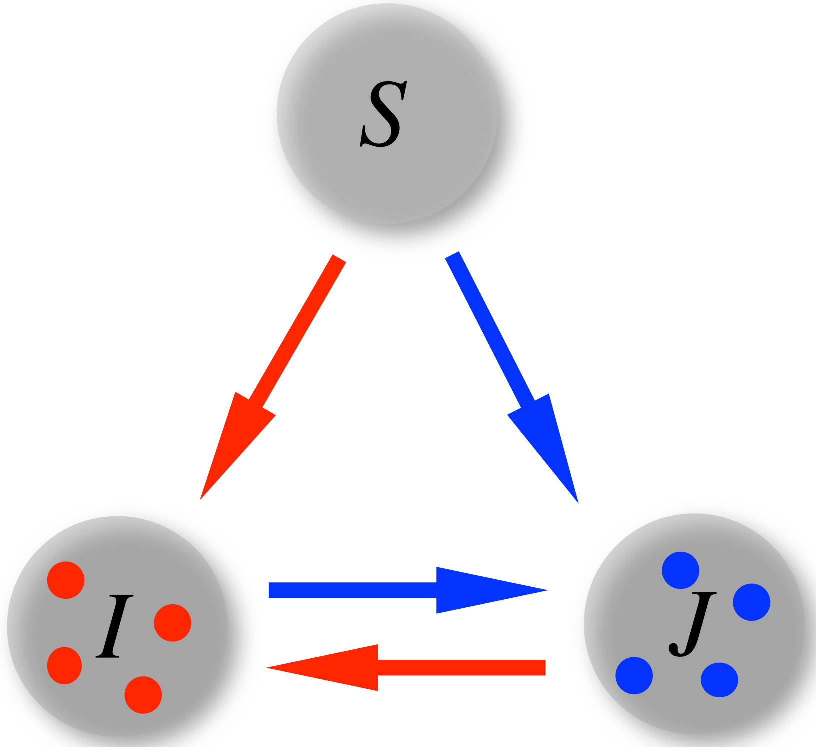
Infections multiples

- parasites partagent leurs hôtes
- reduit transmission en long terme
- favorise transmission en court terme
- mène à une virulence augmentée
  - Eshel 1977
  - Levin & Pimentel 1981
  - Nowak & May 1994
  - van Baalen & Sabelis 1995

Modèles compétition intra-hôte

- Superinfection
  - la souche la plus virulente remplace les autres
    - (Levin & Pimentel 1981, Nowak & May 1994)
  - chaque souche a une chance de gagner
    - Gandon et al. 2001, 2002)
- Coinfection
  - les souches coexistent à l’intérieur de l’hôte
    - (Eshel 1977, van Baalen & Sabelis 1995)

Superinfection



Superinfection

σ : Aggressivité intra-hôte

Invasion

le mutant envahit si

$$\frac{\beta^* \bar{S} + \sigma\beta^* \bar{I}}{\mu + \alpha^* + \sigma\beta\bar{I}} > 1$$

fitness ≠ taux de reproduction de base !

$$R_0 = \frac{\beta^* \bar{S}}{\mu + \alpha^*}$$

`

- virulence optimale maximise

$$\frac{\beta^* \bar{S} + \sigma\beta^* \bar{I}}{\mu + \alpha^* + \sigma\beta\bar{I}}$$

- en contraste avec cas simple, dépend de plein de choses
  - densité hôtes saines,
  - densité hôtes infectés (avec souche residente)
  - stratégie de la souche residente

Cas simple

- supposons σ constant
- virulence optimale maximise

$$\frac{\beta}{\mu + \alpha + \sigma\beta^{*}\bar{I}}$$

- presque comme résultat déjà obtenu, sauf que virulence dépend du ‘force d’infection’ du resident ($\beta^{*} I$)

Résumé

Modèle simple sans compétition intra-hôte :
- pas de « virulence management »

Avec compétition intra-hôte :

- infection difficile → moins d'infections multiples

- moins d'infections multiples → virulence diminuée

Ewald:
« C'est ce que je dis tout le temps ! »

Virulence & infections multiples

niveau populationnel

interactions sociales, interactions ecologiques, compétition, ressources, santé publique

niveau individuel

infectivité, mortalité, immunité, comportement, visites médicales, vaccination

niveau intra-hôte

physiologie, dynamique intra-hôte, aspects moléculaires, médication