Centre de formation sur l'environnement et la société

UE Introduction à l'écologie du développement durable

1: The tragedy of the commons

Enseignant : David Claessen

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16 février 2016

The author is professor of biology, University of California, Santa Barbara. This article is based on a presidential address presented before the meeting of the Pacific Division of the American Association for the Advancement of Science at Utah State University, Logan, 25 June 1968.

13 DECEMBER 1968

The Tragedy of the Commons

The population problem has no technical solution; it requires a fundamental extension in morality.

Garrett Hardin

At the end of a thoughtful article on the future of nuclear war, Wiesner and York (*1*) concluded that: "Both sides in the arms race are . . . confronted by the dilemma of steadily increasing military sional judgment. . . ." Whether they were right or not is not the concern of the present article. Rather, the concern here is with the important concept of a class of human problems which can be

What Shall We Maximize?

Population, as Malthus said, naturally tends to grow "geometrically," or, as we would now say, exponentially. In a finite world this means that the per capita share of the world's goods must steadily decrease. Is ours a finite world?

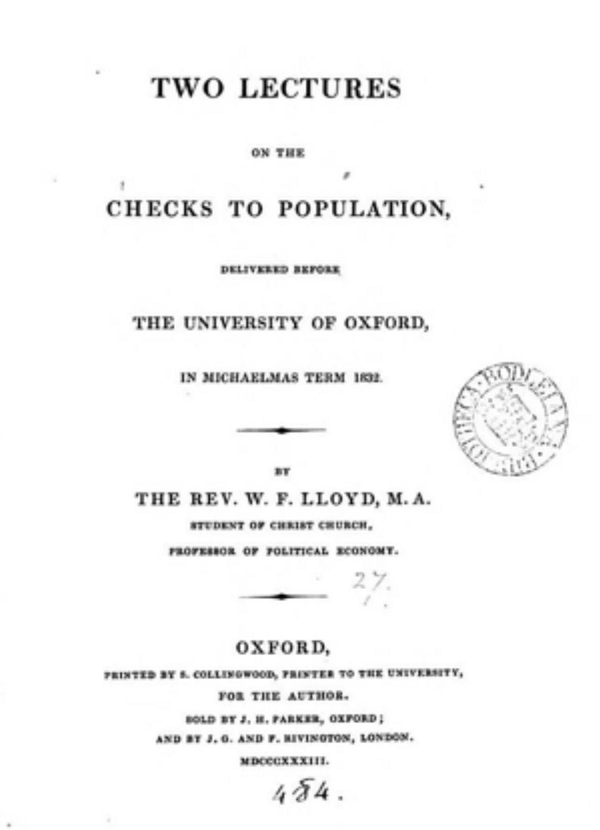
A fair defense can be put forward for the view that the world is infinite; or that we do not know that it is not. But, in terms of the practical problems that we must face in the next few generations with the foreseeable technology, it is clear that we will greatly increase human misery if we do not, during the immediate future, assume that the world available to the terrestrial human population is finite. "Space" is no escape (*2*).

A finite world can support only a finite population; therefore, population growth must eventually equal zero. (The

It is fair to say that most people who anguish over the population problem are trying to find a way to avoid the evils of overpopulation without relinquishing any of the privileges they now enjoy. They think that farming the seas or developing new strains of wheat will solve the problem—technologically. I try to show here that the solution they seek cannot be found.

The « commons »

- « Common » = « village green »



TWO LECTURES

ON THE

CHECKS TO POPULATION,

DELIVERED BEFORE

THE UNIVERSITY OF OXFORD,

IN MICHAELMAS TERM 1832.

BY

THE REV. W. F. LLOYD, M. A.

STUDENT OF CHRIST CHURCH,

PROFESSOR OF POLITICAL ECONOMY.

27.

OXFORD,

PRINTED BY S. COLLINGWOOD, PRINTER TO THE UNIVERSITY,

FOR THE AUTHOR.

SOLD BY J. H. PARKER, OXFORD;

AND BY J. G. AND F. RIVINGTON, LONDON.

MDCCCXXXIII.

484.

William Forster Lloyd (1833)

- Pasturelands left open to many herds of cattle with **a resource available to all**,
- the **greediest** herdsmen would gain—**for a while**
- **Mutual ruin** was just around the corner.
- As demand grew in step with population (while supply remained fixed), a time would come when the herdsmen, acting as Smithian individuals, would be trapped by their own competitive impulses.
- The **unmanaged commons** would be ruined by **overgrazing**

As a rational being, each herdsman seeks to maximize his gain. Explicitly or implicitly, more or less consciously, he asks, "What is the utility *to me* of adding one more animal to my herd?"

This utility has one negative and one positive component.

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1) The positive component is a function of the increment of one animal. Since the herdsman receives all the proceeds from the sale of the additional animal, the positive utility is nearly +1.

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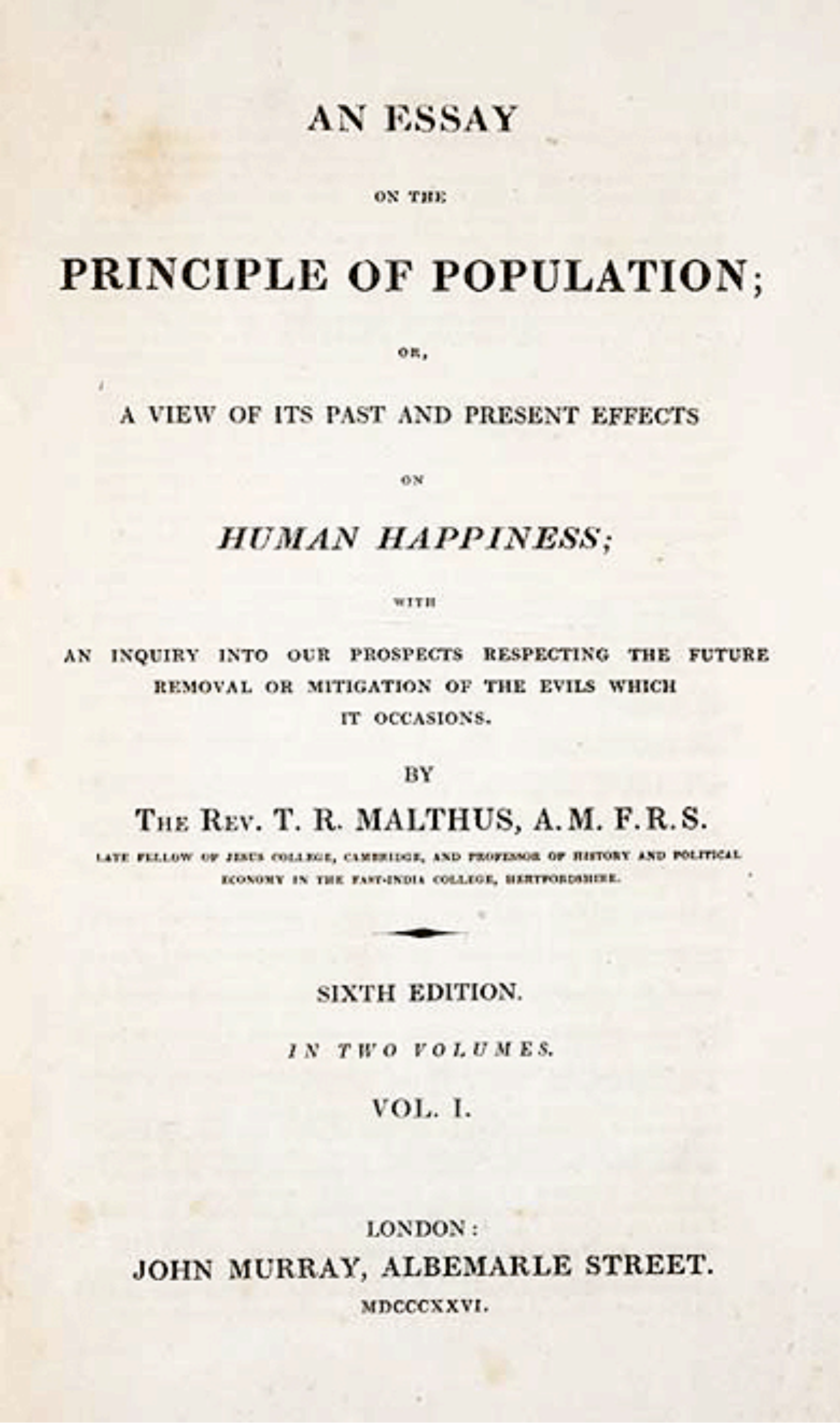
1) The positive component is a function of the increment of one animal. Since the herdsman receives all the proceeds from the sale of the additional animal, the positive utility is nearly +1.

2) The negative component is a function of the additional overgrazing created by one more animal. Since, however, the effects of overgrazing are shared by all the herdsmen, the negative utility for any particular decision-making herdsman is only a fraction of −1.

Adding together the component partial utilities, the rational herdsman concludes that the only sensible course for him to pursue is to add another animal to his herd. And another; and another. . . . But this is the conclusion reached by each and every rational herdsman sharing a commons. Therein is the tragedy. Each man is locked into a system that compels him to increase his herd without limit—in a world that is limited. Ruin is the destination toward which all men rush, each pursuing his own best interest in a society that believes in the freedom of the commons. Freedom in a commons brings ruin to all.

D'où vient le problème?



AN ESSAY

ON THE

PRINCIPLE OF POPULATION;

OR,

A VIEW OF ITS PAST AND PRESENT EFFECTS

ON

HUMAN HAPPINESS;

WITH

AN INQUIRY INTO OUR PROSPECTS RESPECTING THE FUTURE REMOVAL OR MITIGATION OF THE EVILS WHICH IT OCCASIONS.

BY

THE REV. T. R. MALTHUS, A.M. F.R.S.

LATE FELLOW OF JESUS COLLEGE, CAMBRIDGE, AND PROFESSOR OF HISTORY AND POLITICAL ECONOMY IN THE EAST-INDIA COLLEGE, HERTFORDSHIRE.

SIXTH EDITION.

IN TWO VOLUMES.

VOL. I.

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
MDCCCXXVI.

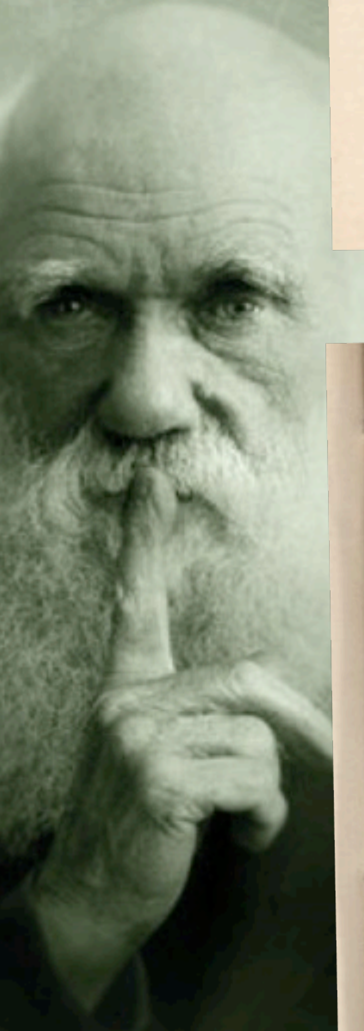
Thomas Robert Malthus

- **Geometrical population growth**
- The increase of population is necessarily **limited** by the means of subsistence;
- The superior power of population is repressed, and the actual population kept equal to the means of subsistence, by misery and vice.

Inspired by Malthus, Charles Darwin (1859) identified the « struggle for existence »,

in combination with heritable variation,

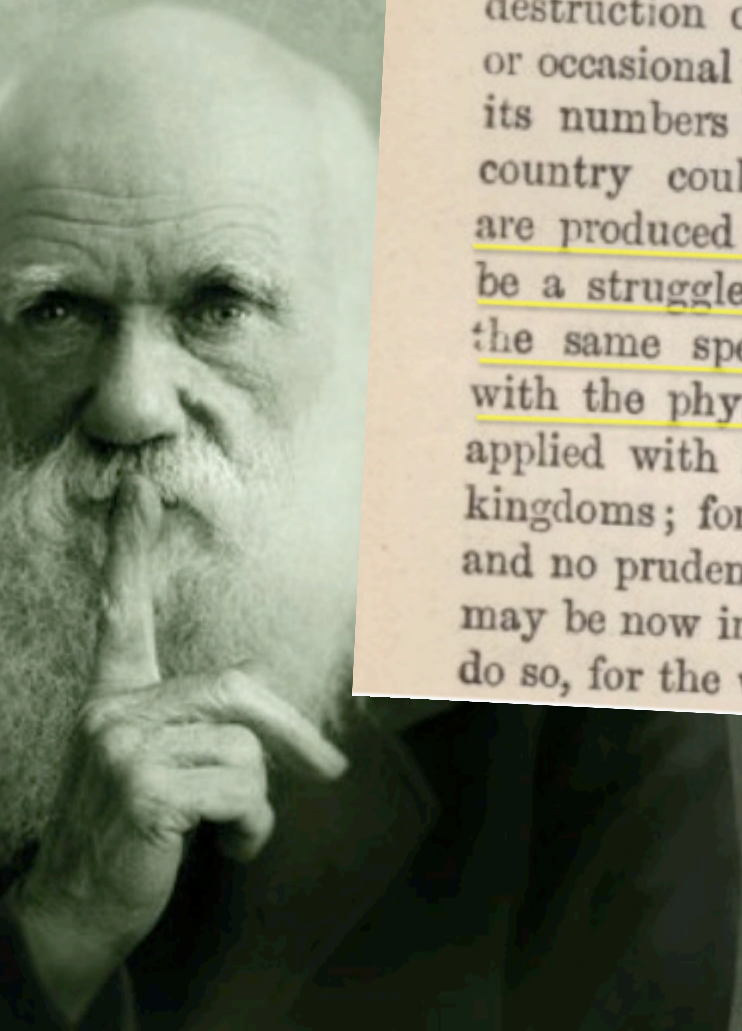
as the driving force of **evolutionary change**.



organic world.

Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct

genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow from the struggle for life. Owing to this struggle, variations, however slight, and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals, and will generally be inherited by the offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species



Geometrical Ratio of Increase.

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them.

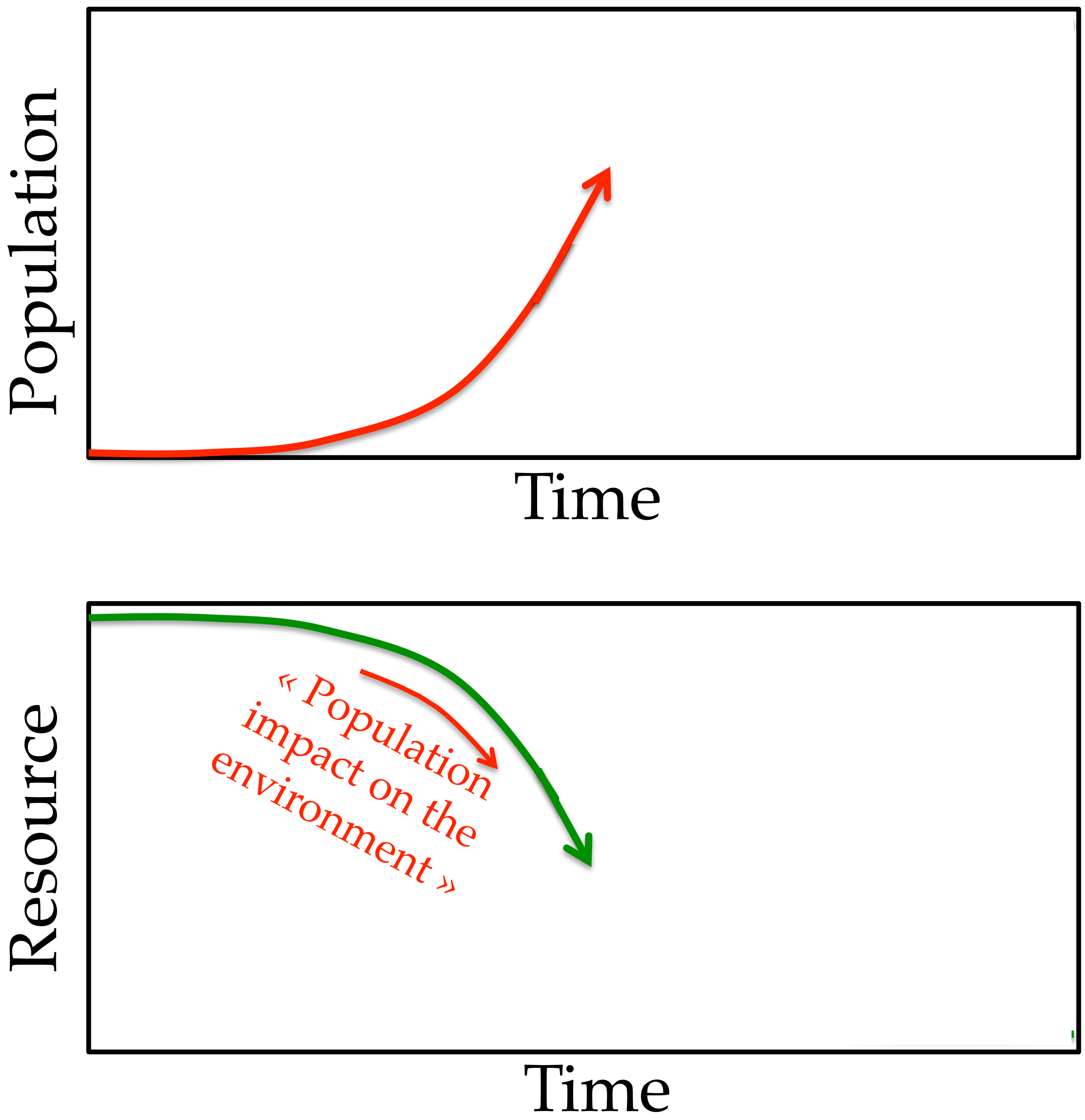
The Complete Work of Charles Darwin Online (http://darwin-online.org.uk/)

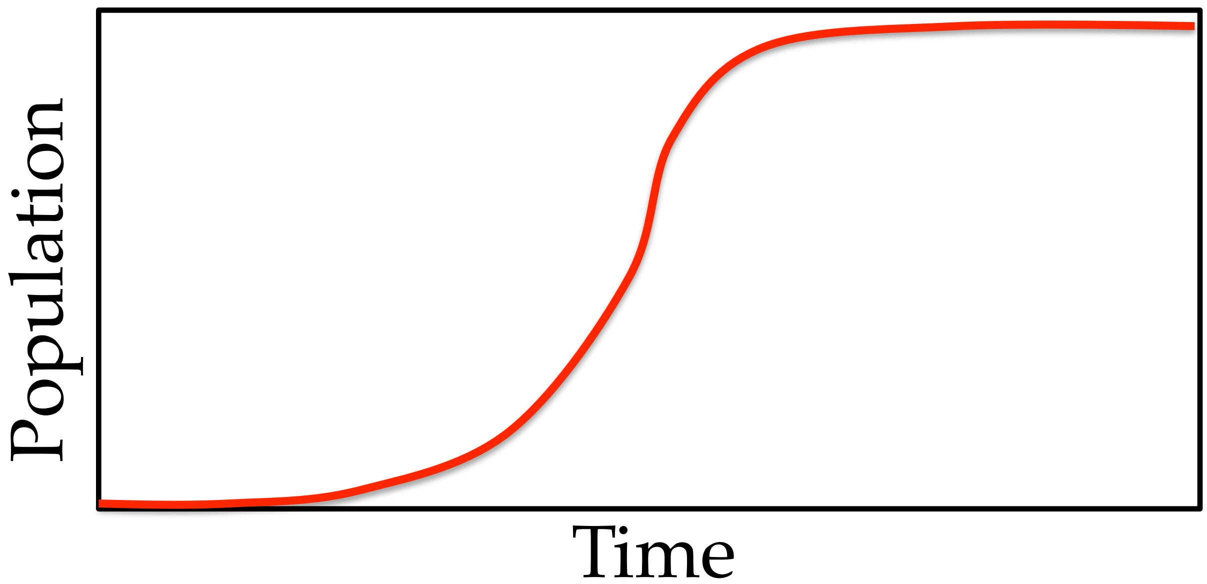
Struggle for existence

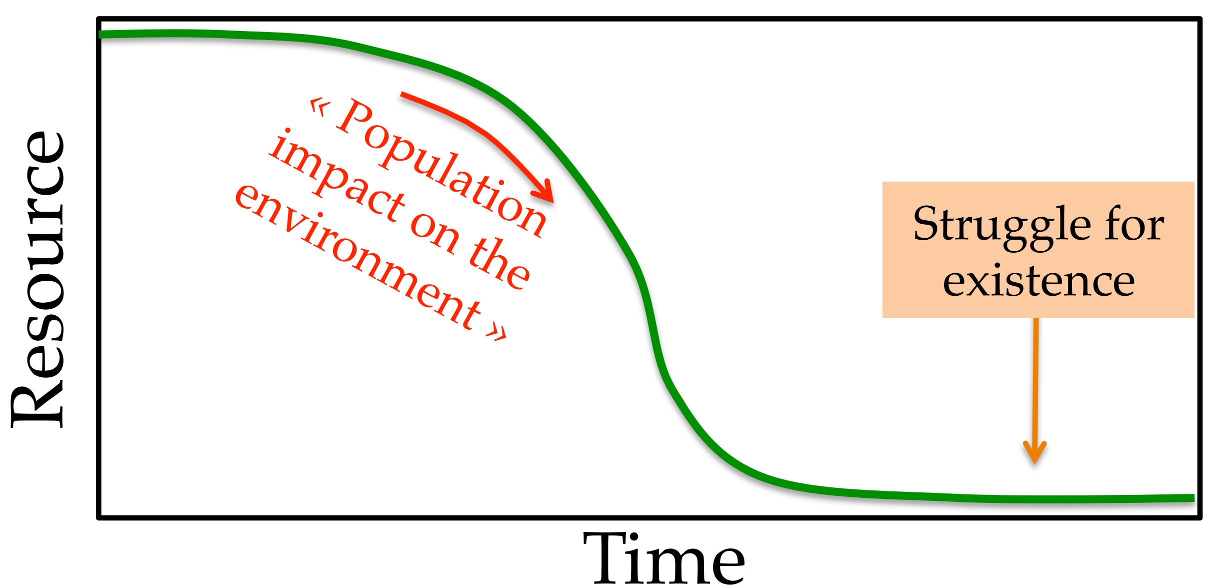
- As a population grows exponentially, its impact on the environment is such that conditions get less favorable for population growth

- This results in population regulation

- In combination with heritable variation, this also results in natural selection
(or: survival of the fittest)

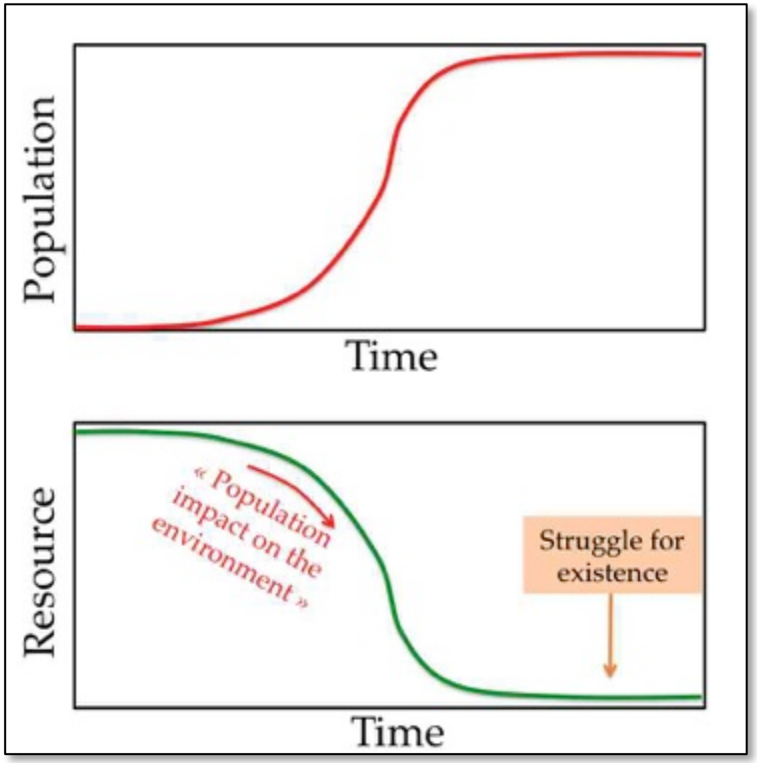

Population
Time
Resource
« Population impact on the environment »
Time


Population
Time


Resource
« Population
impact on the
environment »
Struggle for
existence
Time

Feedback loop

- The struggle for existence corresponds to a feedback loop:
  - The environmental conditions determine the population growth rate
  - The population size determines the environmental conditions



$$\dot{S} = S\left(\frac{aS}{1+S} - b - cS\right) - \theta S X,$$
$$\dot{X} = X(\eta\theta S - \mu).$$

S = resource
X = consumer population abundance

$$\boxed{\text{Fitness W} = \eta\theta S - \mu}$$

Fitness is defined as the
per capita exponential growth rate

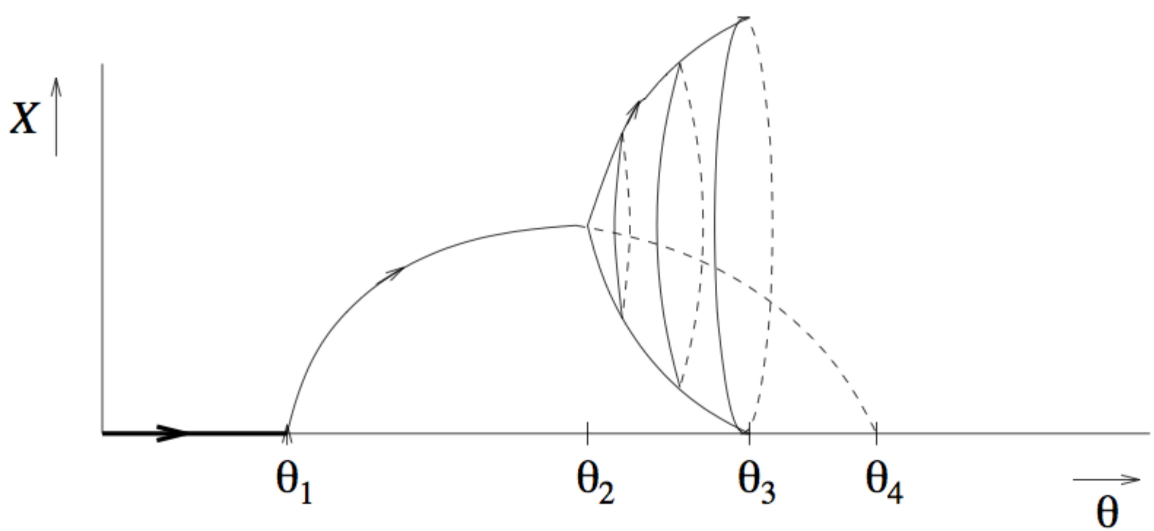
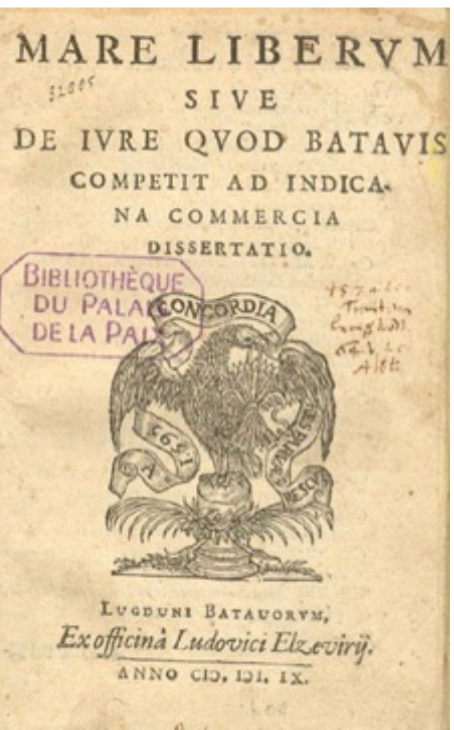


Fig. 8. Bifurcation diagram for (6.1). The adaptive dynamical increase of θ is indicated by the arrows (but, admittedly, the arrow between 0 and θ_1 is meaningless).

D'où vient le problème?

II

1609, Hugo de Groot
(*Hugo Grotius*) :
“The freedom of the seas”



MARE LIBERVM
SIVE
DE IVRE QVOD BATAVIS
COMPETIT AD INDICA-
NA COMMERCIA
DISSERTATIO.

CONCORDIA

LVGDVNI BATAVORVM,
Ex officinâ Ludovici Elzevirij.
ANNO CIↃ. IↃI. IX.

« Peter Pett and the *Sovereign of the Seas* »
Peter Lely (1637)

HVGONIS GROTII
DE
IVRE BELLI
AC PACIS
LIBRI TRES,
In quibus jus Naturæ & Gentium, item juris publici præcipua explicantur.
EDITIO NOVA
AMSTELDAMI,
Apud IOH. & CORNELIVM BLAEV.

1625, **Hugo de Groot** (*Hugo Grotius*) :
“The extent of the ocean is in fact so great that it suffices for any possible use on the part of all peoples for drawing water, for fishing, for sailing.”

“Probably all great sea-fisheries are inexhaustible”

– 1884-Sir Thomas Huxley

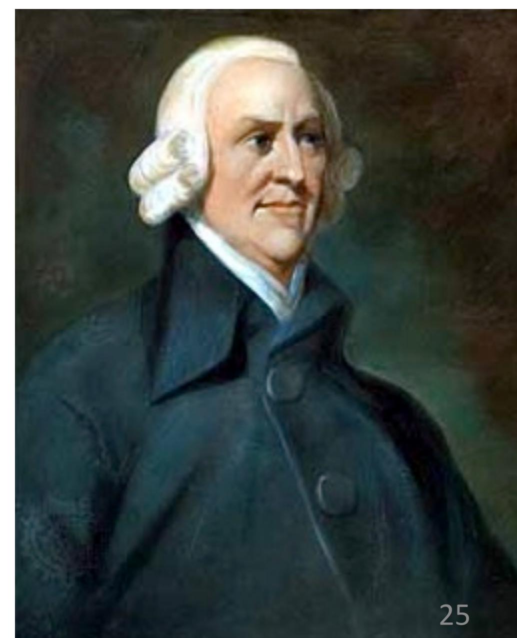
« I know the human being and fish can coexist peacefully »

Saginaw, Michigan; September 29, 2000

« Freedom of the seas » in combination with « the invisible hand » (Adam Smith 1776)

→Tragedy of the commons

In economic affairs, *The Wealth of Nations* (1776) popularized the "invisible hand," the idea that an individual who "intends only his own gain," is, as it were, "led by an invisible hand to promote . . . the public interest"



Rapid worldwide depletion of predatory fish communities

Ransom A. Myers & Boris Worm

Oceanic ecosystems

Shelf ecosystems

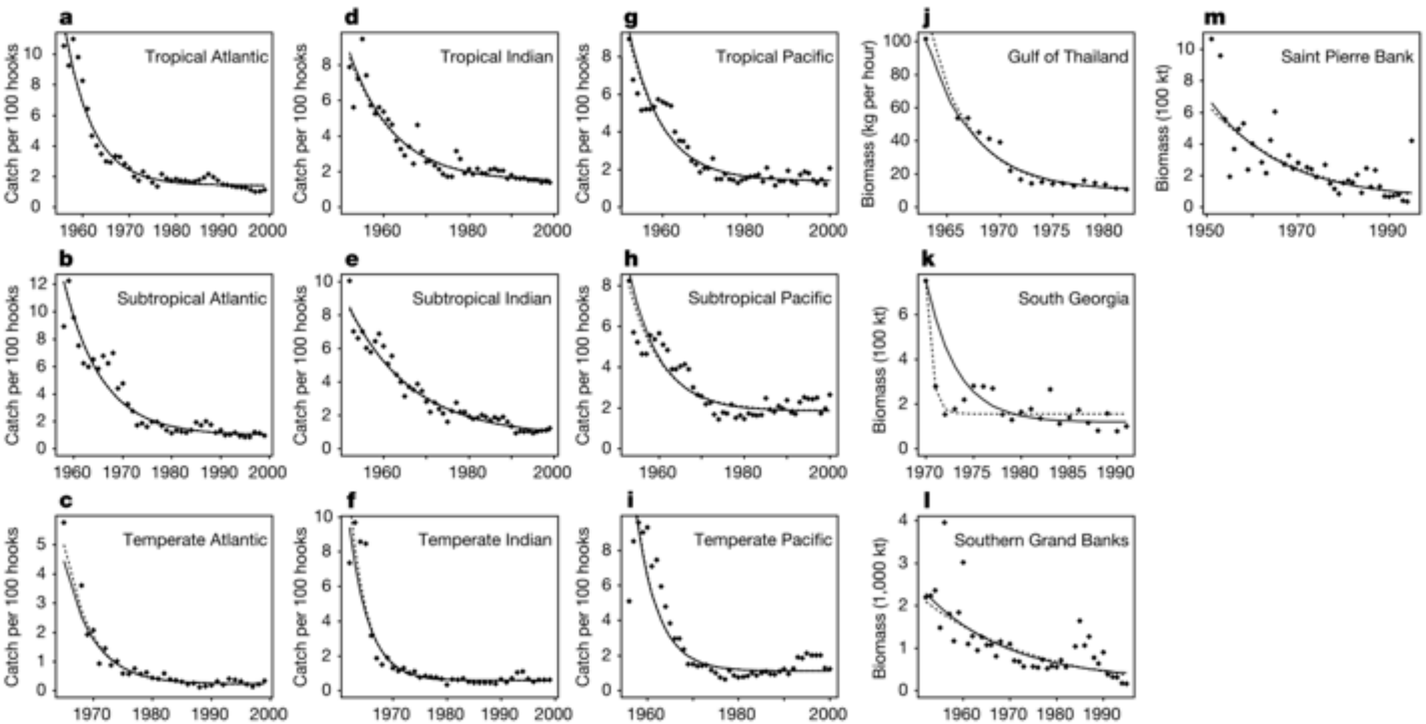


Figure 1 Time trends of community biomass in oceanic (**a–i**) and shelf (**j–m**) ecosystems. Relative biomass estimates from the beginning of industrialized fishing (solid points) are shown with superimposed fitted curves from individual maximum-likelihood fits (solid lines) and empirical Bayes predictions from a mixed-model fit (dashed lines).

Rapid worldwide depletion of predatory fish communities

Ransom A. Myers & Boris Worm

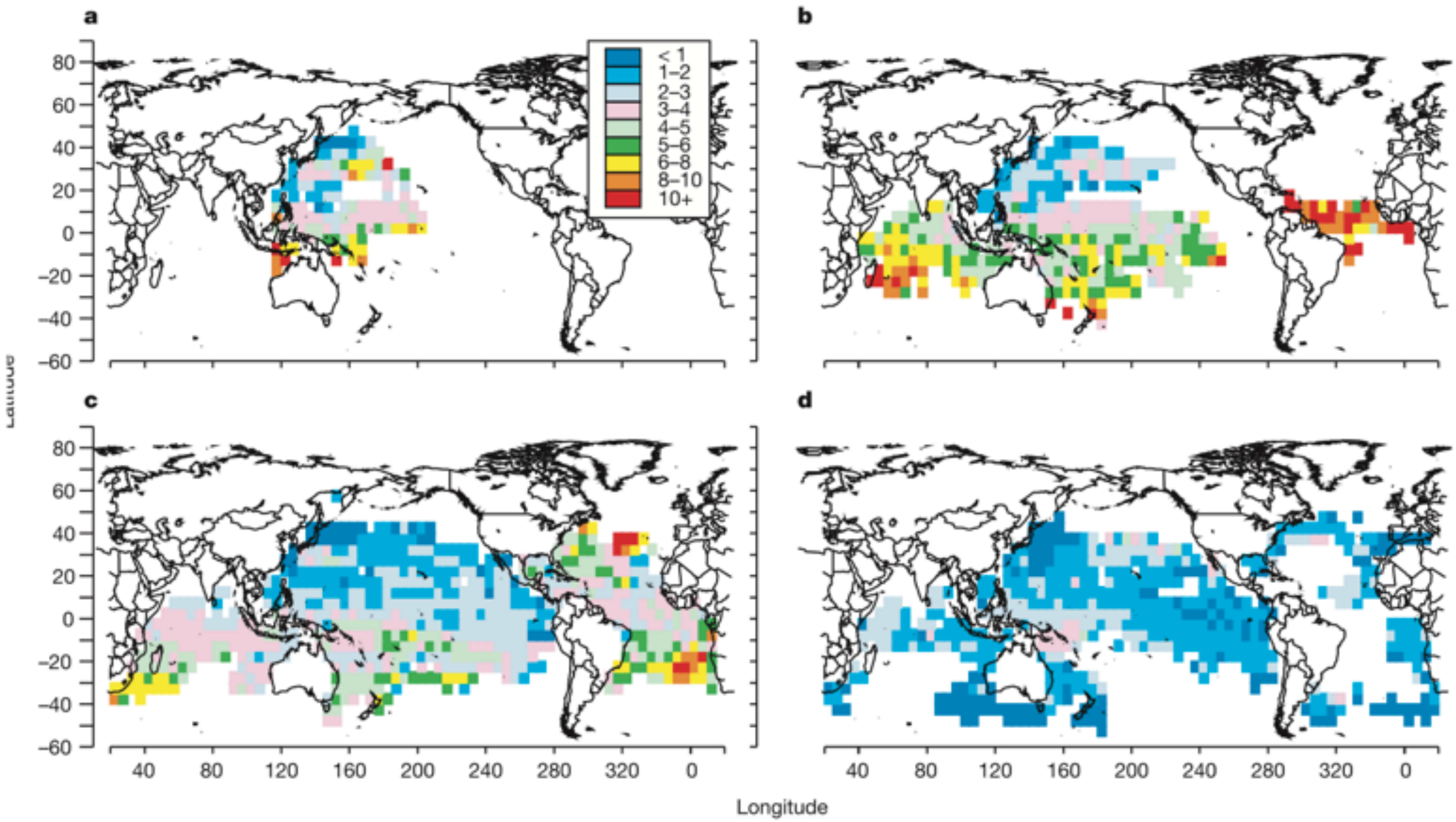
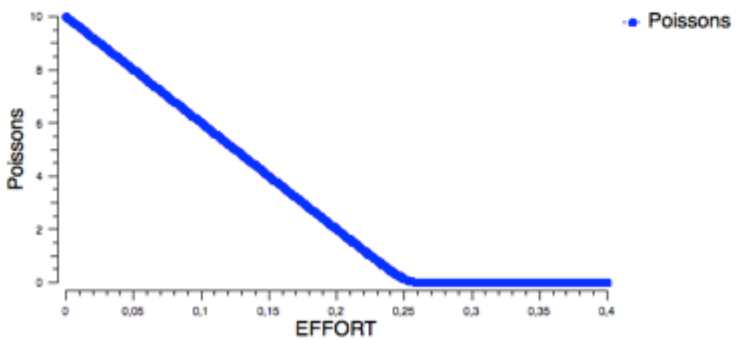
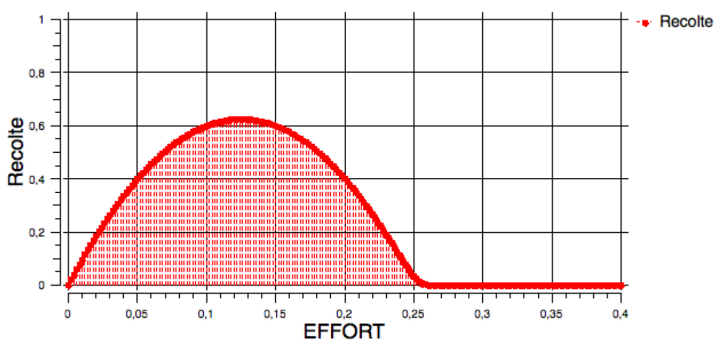


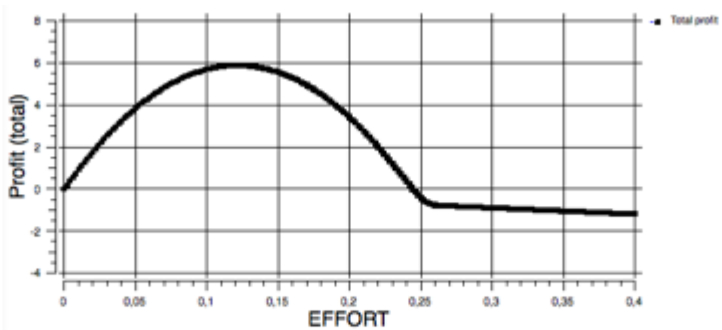
Figure 2 Spatial patterns of relative predator biomass in 1952 (**a**), 1958 (**b**), 1964 (**c**) and 1980 (**d**). Colour codes depict the number of fish caught per 100 hooks on pelagic longlines set by the Japanese fleet. Data are binned in a global 5° × 5° grid. For complete year-by-year maps, refer to the Supplementary Information.

A simple model for fishers vs fish dynamics

L'équilibre :

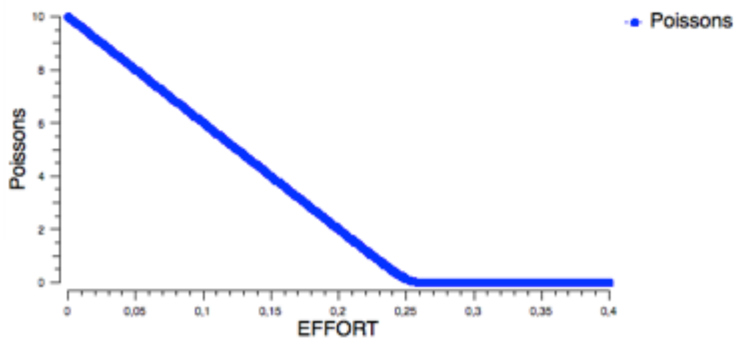


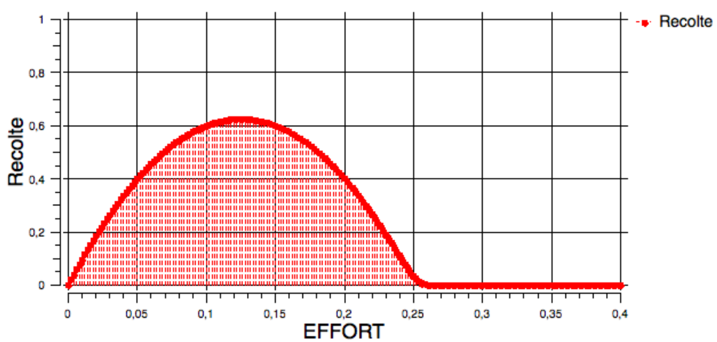


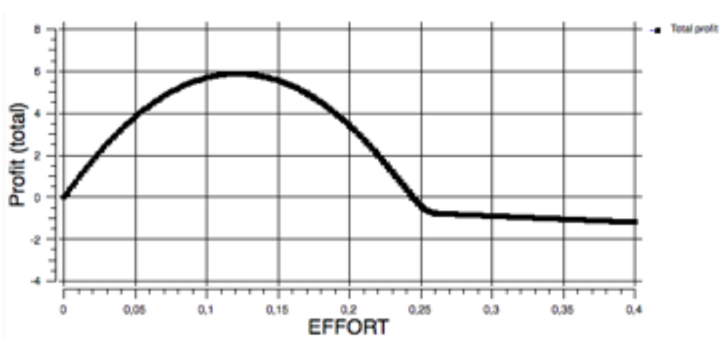


A simple model for fishers vs fish dynamics

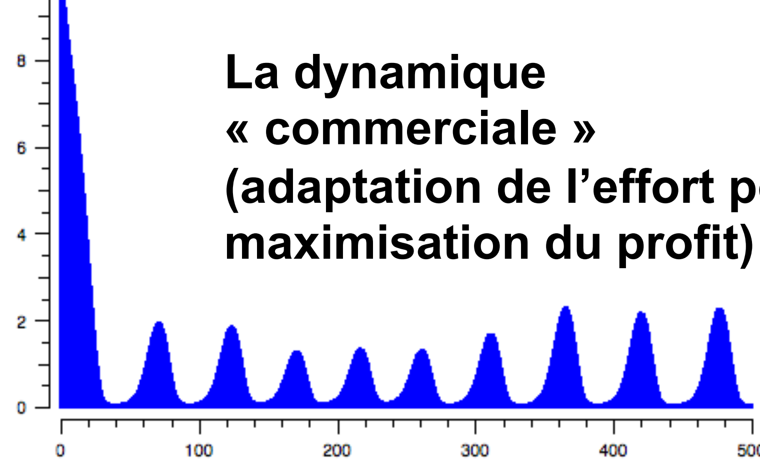
L'équilibre :

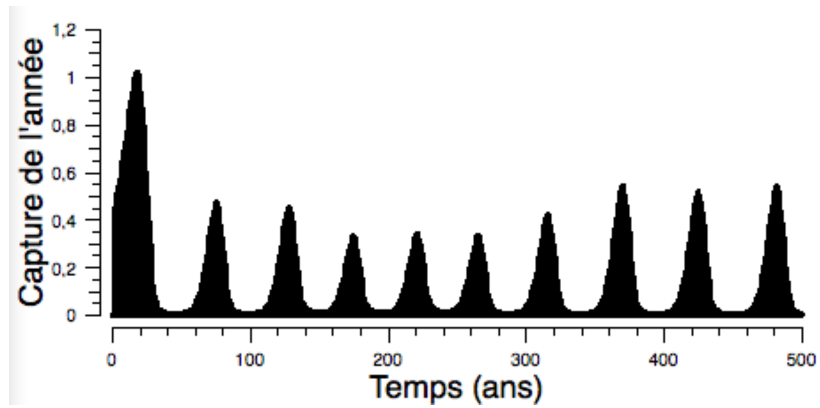


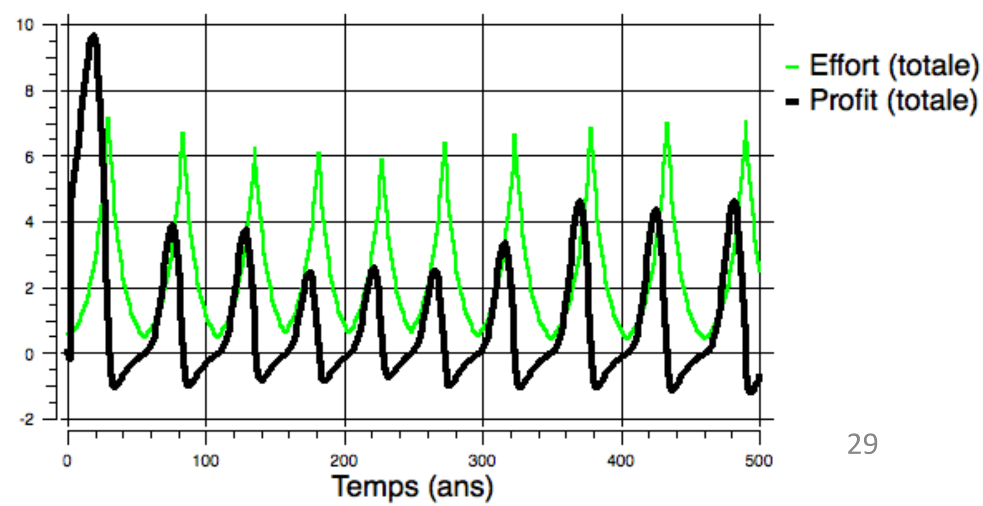




La dynamique « commerciale » (adaptation de l'effort pour maximisation du profit)







The tragedy of the commons

- Individual maximisation of profit, where
  - benefit is individual
  - while the cost is shared
- Short term thinking

- Solutions?
  - Cooperation
  - Privitization
  - Nationalisation

- How can cooperation evolve in the face of the « tragedy of the commons » ?
  - Examples from ecology

The emergence of
the tragedy of the commons
in an ecological system:

evolution of **selfish strategies**
that put the population in danger

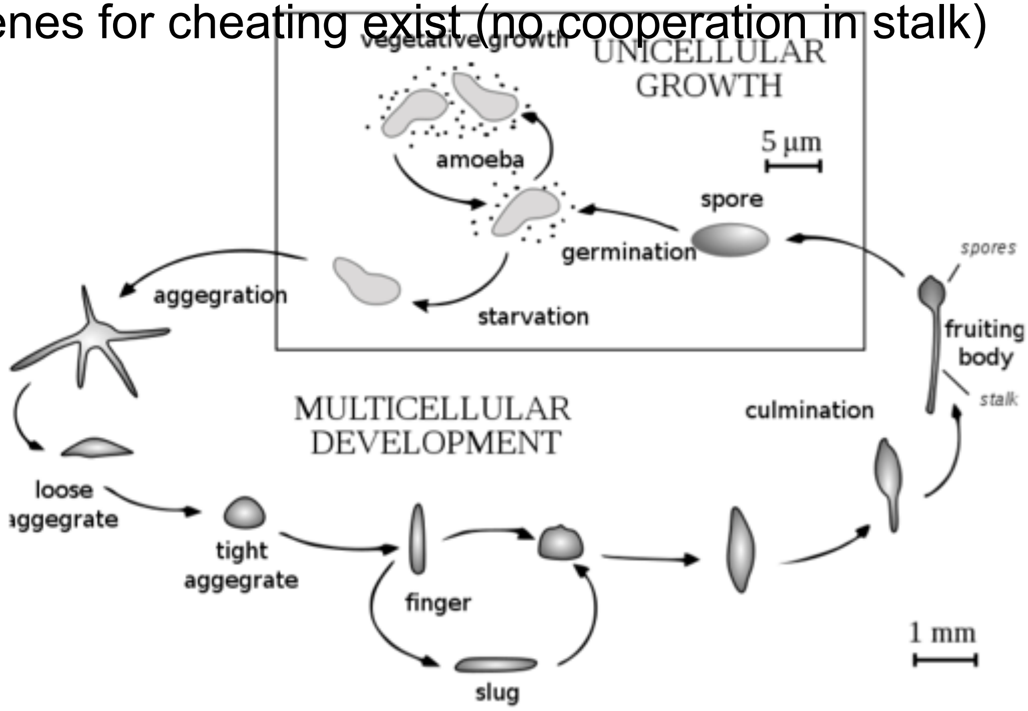
The emergence of cooperation in ecological systems

Évolution de la cooperation

- Comportements « **altruistes** », comment expliquer?
  - Cris d'alarme qui attirent l'attention de conspécifiques sur la survenue d'un predateur mais pourraient orienter celui-ci sur la « sentinelle »
  - Allaitement collectif de la lionne (prive de lait ses propres jeunes)
  - Le renoncement à la reproduction chez les ouvrières d'abeilles ou de fourmis, pour mieux se consacrer à l'élevage de la descendance d'une reine

Dictyostelium discoideum

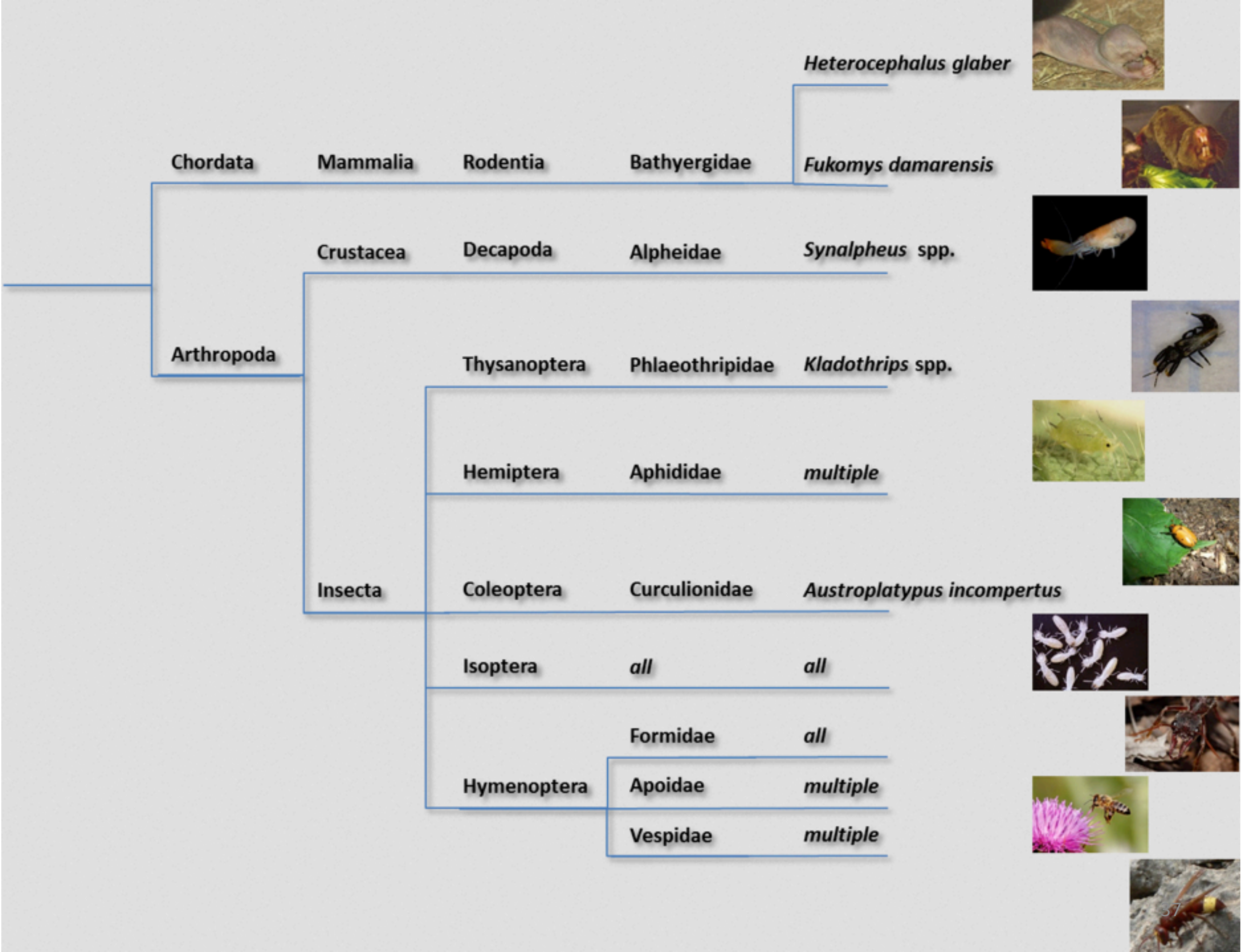
Unicellular amoeba
Multicellular development → spores production & migration
Only a fraction of cells delivers genetic material to spores
Majority of cells « sacrifices » themselves by forming the stalk
Why?
Genes for cheating exist (no cooperation in stalk)



Type of adult bee	What they do	How many in a honey bee colony	How many in a bumble bee colony	What they look like in a honey bee colony	What they look like in a bumble bee colony
Queen	Lay eggs	1	1		
Worker	Take care of larvae, build and clean nest, forage	10,000-50,000	Less than 50 to over 400, depending on species		
Male	Leave nest to mate, then die	100-500	0-50, depending on species and season		

Evolution de la socialité

- Degrés dans l'évolution de la socialité, les stades
  - **Solitaire**
  - **Grégaire** (interattraction; phéromones)
  - **Sub-social** (comportements parentaux)
  - **Colonial** (soins au jeunes en élevage commun à plusieurs femelles, sans coopération)
  - **Communal** (colonial + coopération)
  - **Social (eusocial)** (communal + spécialisation de la reproduction : division du travail)


Chordata
Mammalia
Rodentia
Bathyergidae
Heterocephalus glaber
Fukomys damarensis
Arthropoda
Crustacea
Decapoda
Alpheidae
Synalpheus spp.
Insecta
Thysanoptera
Phlaeothripidae
Kladothrips spp.
Hemiptera
Aphididae
multiple
Coleoptera
Curculionidae
Austroplatypus incompertus
Isoptera
all
all
Hymenoptera
Formidae
all
Apoidae
multiple
Vespidae
multiple

Kin selection – Sélection de parentèle

- Darwin about the conundrum represented by altruistic sterile social insects (The Origin of Species, 1859)
  - « *This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that **selection** may be applied to the **family**, as well as to the **individual**, and may thus gain the desired end. Breeders of cattle wish the flesh and fat to be well marbled together. An animal thus characterized has been slaughtered, but the breeder has gone with confidence to the same stock and has succeeded.* »
- RA Fisher (1930), JBS Haldane (1932), WD Hamilton (1963)
- J Maynard Smith (1963) « Kin selection »
  - « These processes I will call **kin selection** and group selection respectively. Kin selection has been discussed by Haldane and by Hamilton. … By kin selection I mean the evolution of characteristics which favour the survival of close relatives of the affected individual, by processes which do not require any discontinuities in the population breeding structure. »

Haldane

- Question : « Would you lay down your life for your brother? »
- Answer : « No, but I would for two brothers or eight cousins »

Modern synthesists: (left to right) J. B. S. Haldane, Sewall Wright and Ronald Fischer.

r = coefficient de parenté, « *coefficient of relatedness* »

= « le coefficient de proximité génétique entre x et y »

= « the probability that a gene picked randomly from each at the same locus is identical by descent »

= « Le coefficient de parenté entre deux individus, i et j, est égal à la probabilité pour que deux gènes tirés au hasard au même locus, l'un chez i et l'autre chez j, soient identiques par descendance »

Organismes diploïde

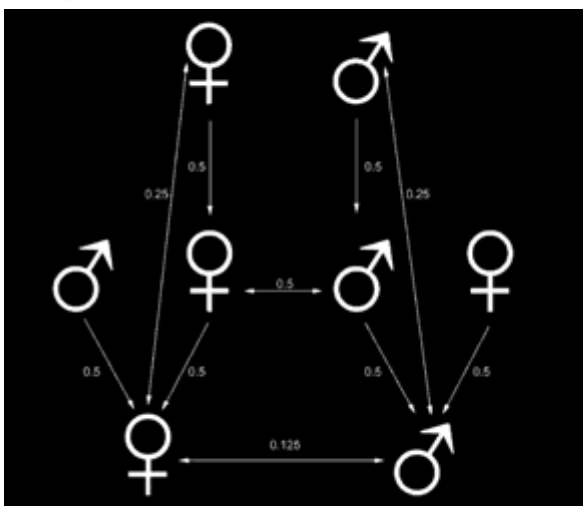
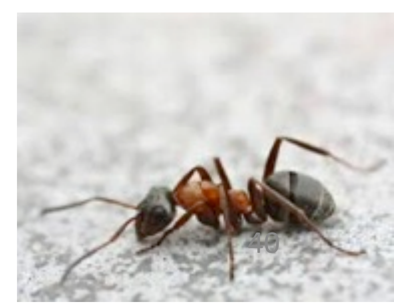


Fig. 1: The coefficient of relatedness. In diploid organisms, every parent (top row) transmits 50% of its genetic information to each offspring (middle row). On the average, siblings therefore share half of each parent's contribution to their genome, adding to a coefficient of relatedness *r*=0.5. Consequently, cousins share an *r*=0.125 or *r*=1/8 (bottom row). Likewise, these cousins are related to their common grandparents by ¼ or *r*=0.25. One may also say that *r* is a measure for the probability that any given allele is shared by two individuals.

Organismes haplo-diploïde

	Mère	**Père**	**Sœur**	**Frère**
Fille	1/2	1/2	3/4	1/4
Fils	1/2	0	1/4	1/4



Sélection de parentèle

- La loi de Hamilton
- Altruisme peut évoluer si

$$r\,B > C$$

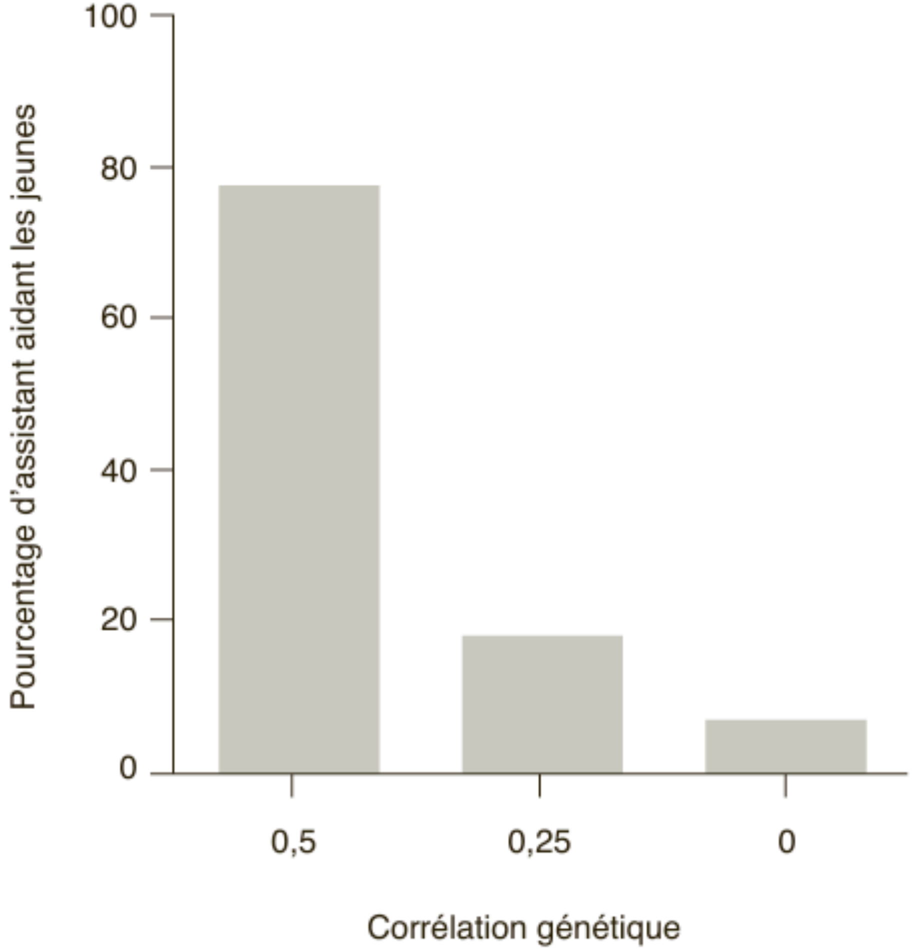
  - *r* est le coefficient d'apparentement
  - *B* est le bénéfice d'altruisme pour l'autre individu
  - *C* est le cout de comportement altruiste

Inclusive fitness

- « Succès reproductif global »

$$S_T = S + b\ r$$

  - *S* succès reproductif immédiat
  - *B* bénéfice d'altruisme
  - *r* la corrélation génétique entre les individus



Sélection de la parentèle chez le geai de Floride.

Lorsque les assistants sont les frères des jeunes, ils aident proportionnellement plus souvent que des demi-frères et ces derniers aident plus que les rares assistants non apparentés (D'après Mumme, 1992, *Behavioral Ecology and Sociobiology*, 31, 319-328).


Three Florida Scrub-Jays (*Aphelocoma coerulescens*) at their nest, 11 May 1977.
Mother (10 yrs. old) and daughter (7 yrs.old) (L-R) are on the nest, father (3 yrs. old) perches above, and the nestlings are 18 days old. Copyright photo by J.W. Fitzpatrick & G.E. Woolfenden.


Florida Jay

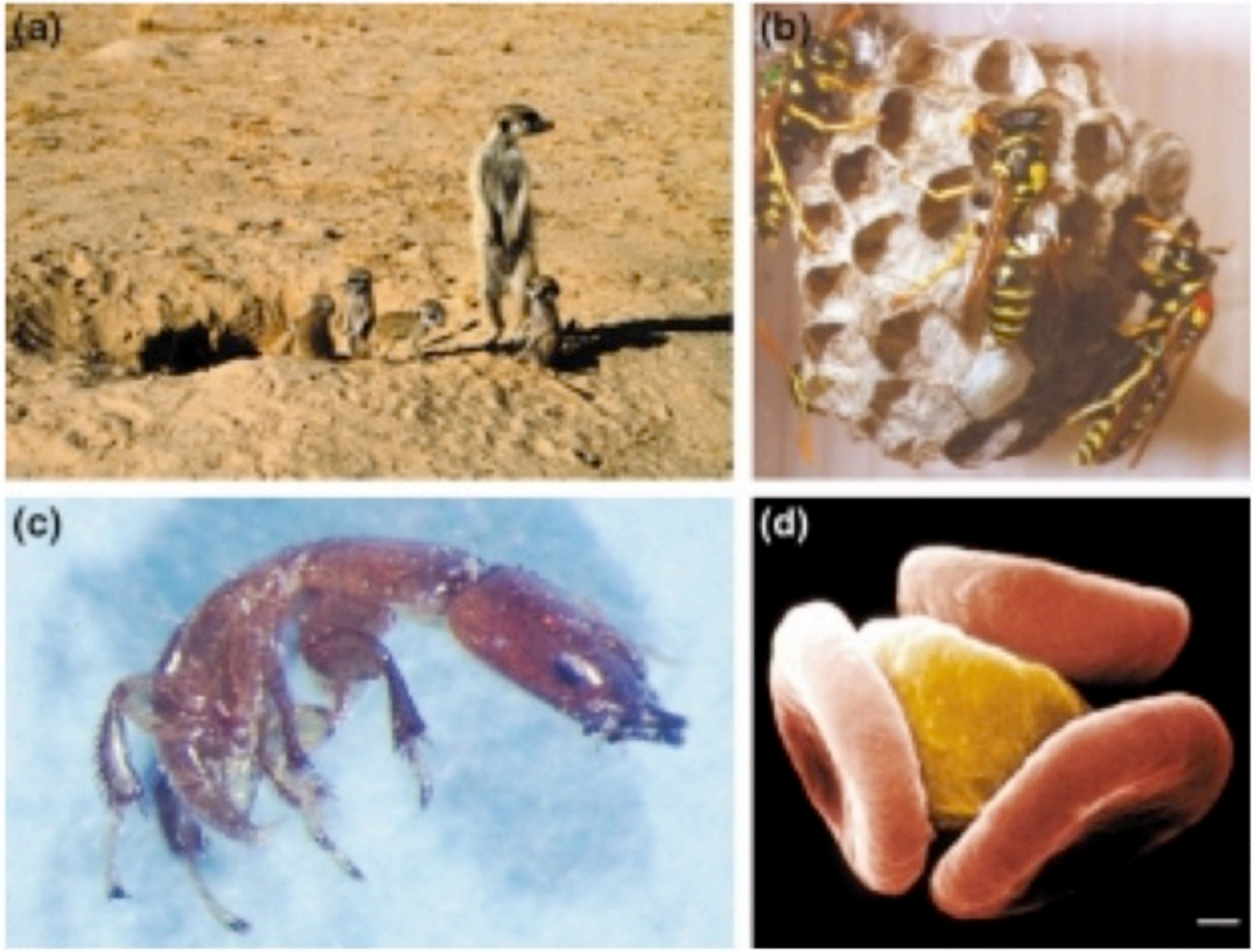
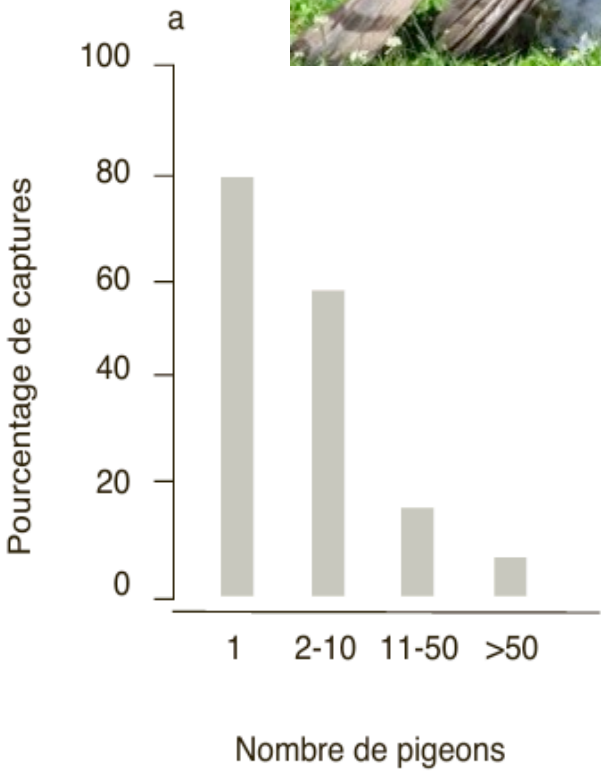
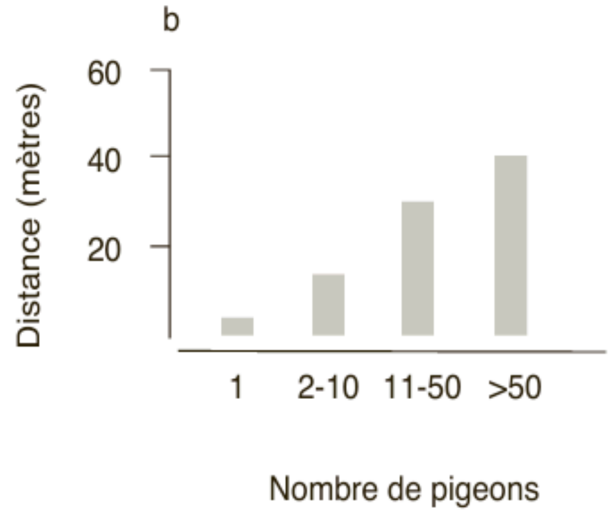


Fig. 1. Examples of species in which kin selection might not be as important as it was previously thought to be. (a) Helping behaviour in meerkats *Suricata suricatta* is not correlated to relatedness [18]. This babysitting subordinate meerkat might not be gaining any fitness through kin selection, but rather increasing its chances of successfully breeding in the future. (b) In the social wasp *Polistes dominulus*, 35% of helpers are unrelated, and benefit from helping by increasing the likelihood of inheriting a nest and worker force [31]. (c) The severity of fighting between male fig wasps is not correlated to relatedness [46]. This is a male *Sycoscaptor australis* wasp, a species in which there is severe fighting, and in which decapitation is common. (d) Scanning electron micrograph of a *Plasmodium falciparum*-infected erythrocyte forming a rosette, a process associated with virulence in human malaria; scale bar = 1 μm. Virulence in malaria parasites does not consistently correlate with relatedness [57]. Photographs, reproduced with permission, from Ashleigh Griffin (a); Joan Strassman (b); James Cook (c); and David Ferguson (d).

Griffin and West, TREE (2002)

But cooperation also occurs in groups of **unrelated** individuals





Bénéfices de la vigilance collective à l’égard des prédateurs
chez le pigeon ramier : (a) pourcentage de captures réussies par un autour
et (b) distance séparant le prédateur du groupe de pigeons
au moment de leur envol, en fonction de l’effectif du groupe de pigeons.
(D’après Kenward, 1978, *Journal of Animal Ecology*, 47, 449-460).

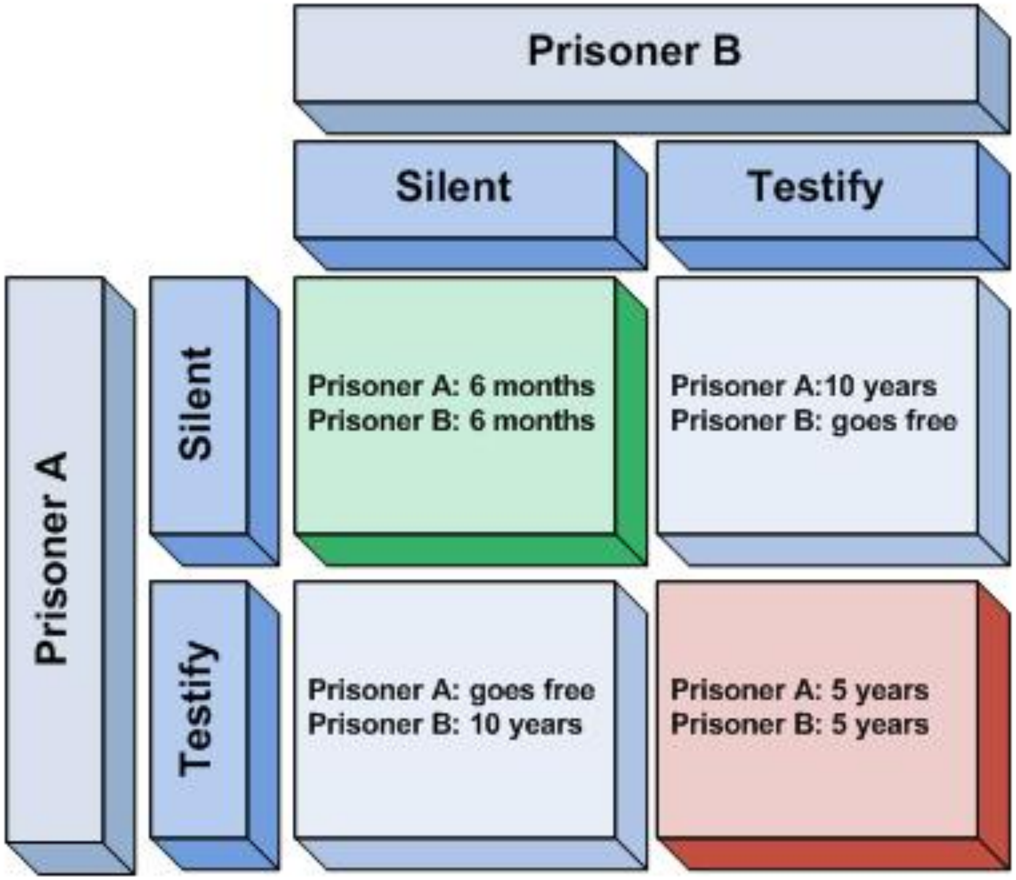
Kin selection **cannot** explain the emergence of altruistic behaviour (**cooperation**) between **unrelated** individuals

What mechanism can?

Altruisme réciproque

- Dilemme du prisonnier
- Théorie des jeux

- « stay silent or rat out the other guy »



$$T > R > P > S$$

- *T = temptation*
- *R = reward (*coopération*)*
- *P = punishment*
- *S = sucker's payoff (*duperie*)*

- *R > P* : coopération est supérieure à défection collective
- T > R et P > S impliquet que la défection est la stratégie dominante

Canonical PD payoff matrix

	Cooperate	**Defect**
Cooperate	*R*, *R*	*S*, *T*
Defect	*T*, *S*	*P*, *P*

« Tit for tat »

- « Equivalent retaliaton »
- Jeu de dilemme de prisonnier **répété**
- Stratégie Tit for tat :
  - Premier tour : coopérer
  - Ensuite, copier le dernier tour de l'adversaire

- Meilleur stratégie dans ce jeu
- L'évolution de **l'altruisme réciproque** ?

Altruisme réciproque

- Une coopération altruiste
  - Aide proposée à perte
  - Expectation de recevoir de l'aide plus tard
  - Bénéfice commun

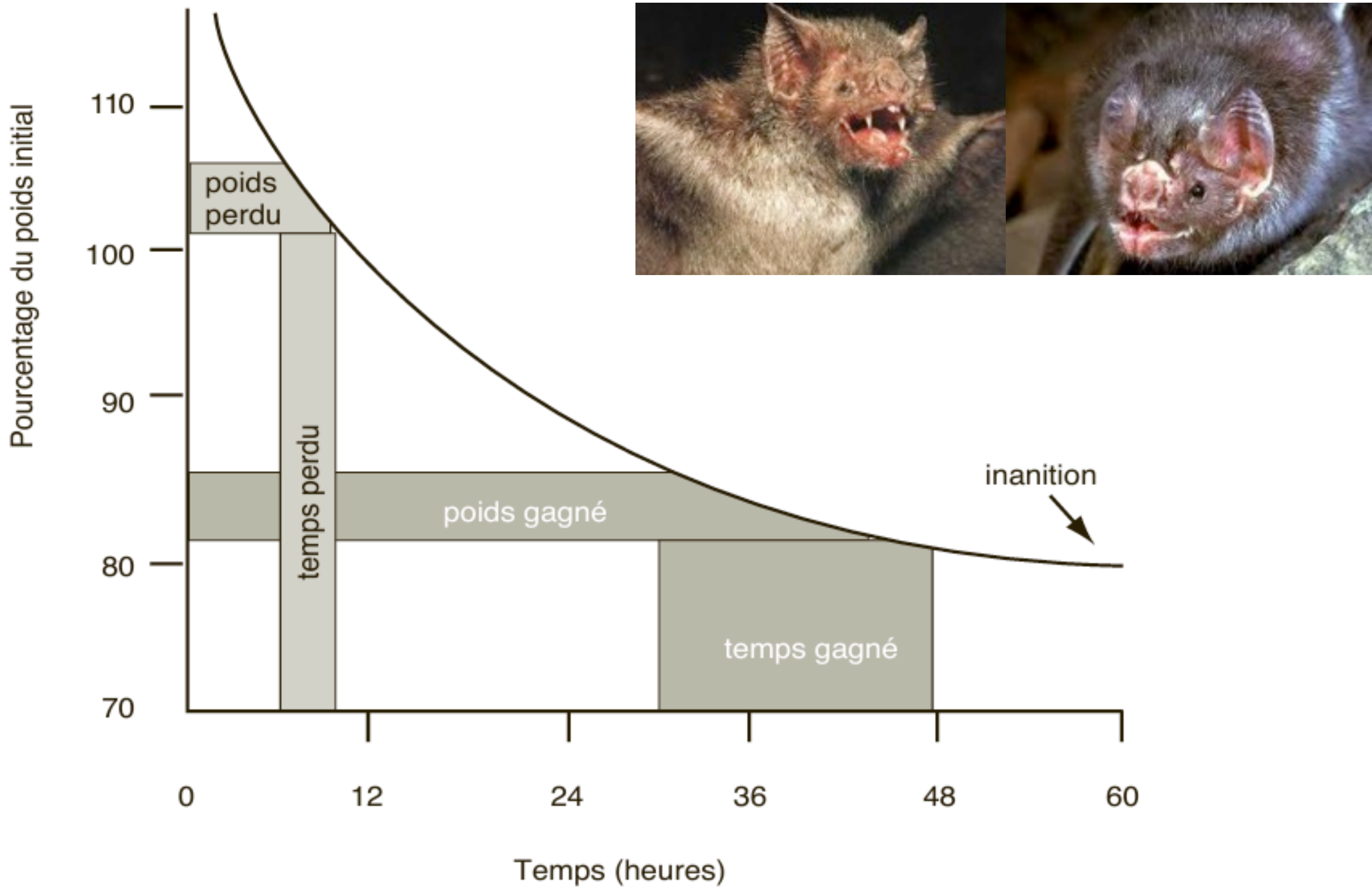
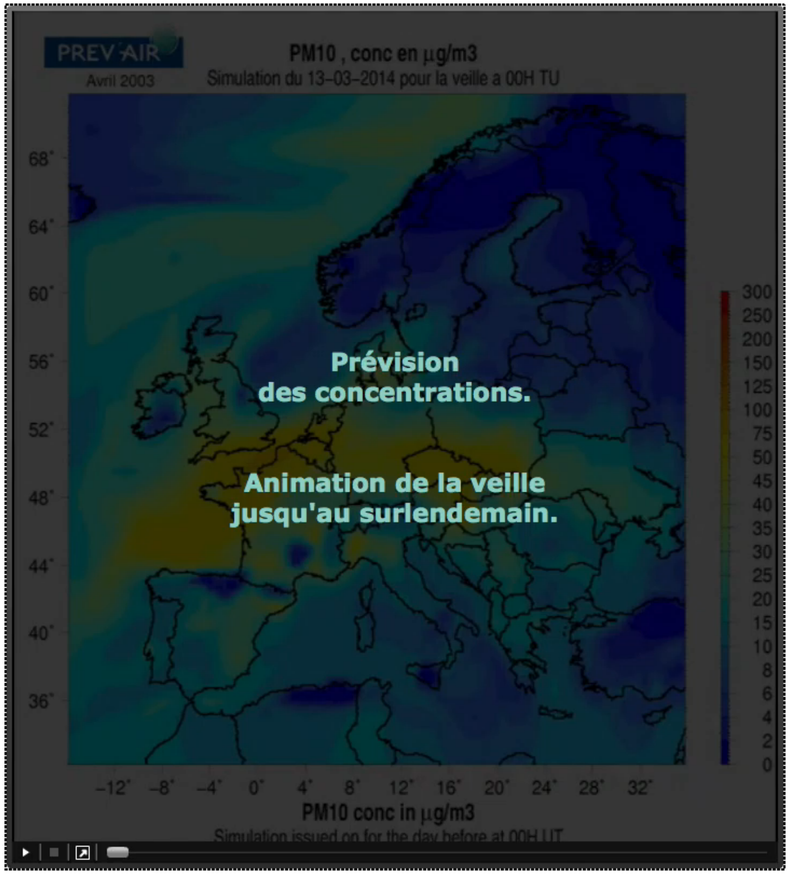


Figure 68 Perte de poids en fonction du temps et réciprocité chez les vampires d'Azara.

Lors d'un échange de sang entre deux individus, le temps d'autonomie dont bénéficie le receveur est supérieur au coût d'un tel échange pour le donneur. Le don de 5 millilitres de sang à un compagnon n'ayant pu s'alimenter pendant 48 h se traduit par une perte de 3 h de réserves alimentaires, mais procure au receveur 18 h de sursis. (Modifié d'après Wilkinson, 1984, *Nature*, 308 : 181-184).

Back to the environment





What can we learn from ecology?

To avert the tragedy;

Cooperation

How to get it?

- Tight feedback loops
- Localised interactions
- « Think locally, act locally »