Modélisation épidémiologique et évolution des traits de vie (ex Nématodes)

Serge Morand (CBGP)

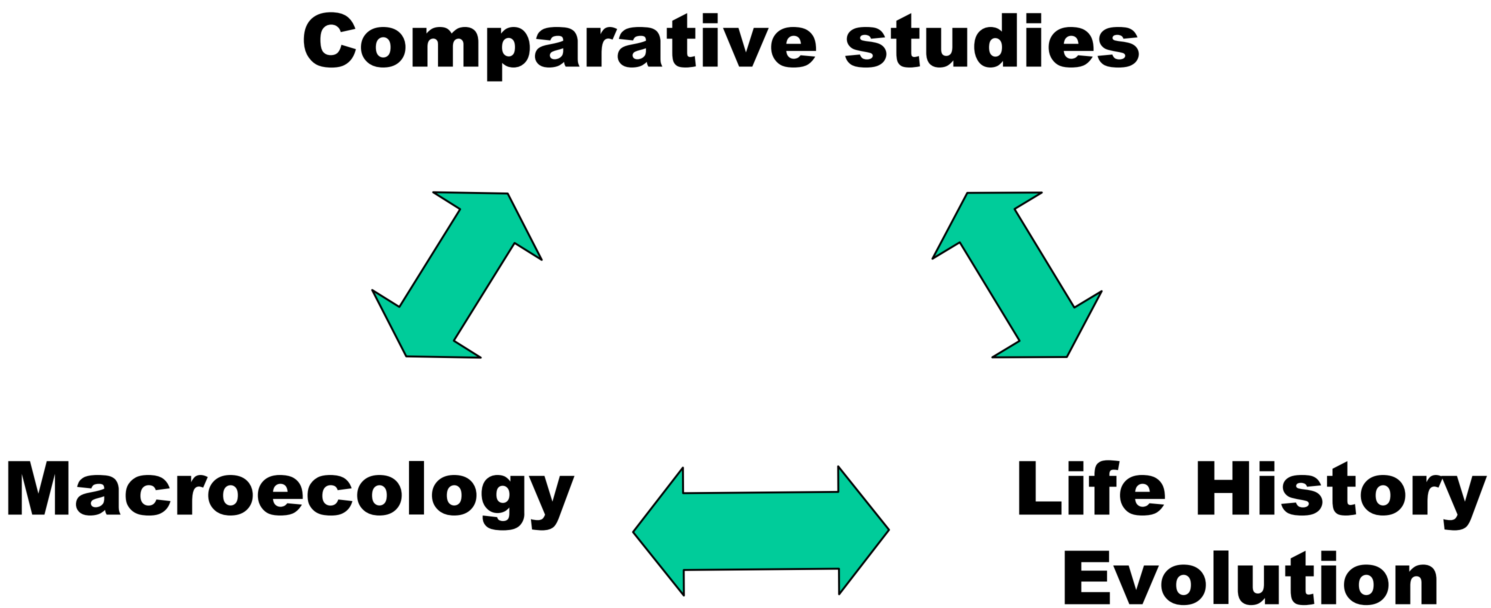
CIRAD
INRA
IRD Institut de recherche pour le développement
agro Montpellier Ecole Nationale Supérieure Agronomique

“PATTERN”

- Species diversity
- Abundance & distribution
- Morphology
- Life traits

“PROCESS”

- Adaptation
- Competition

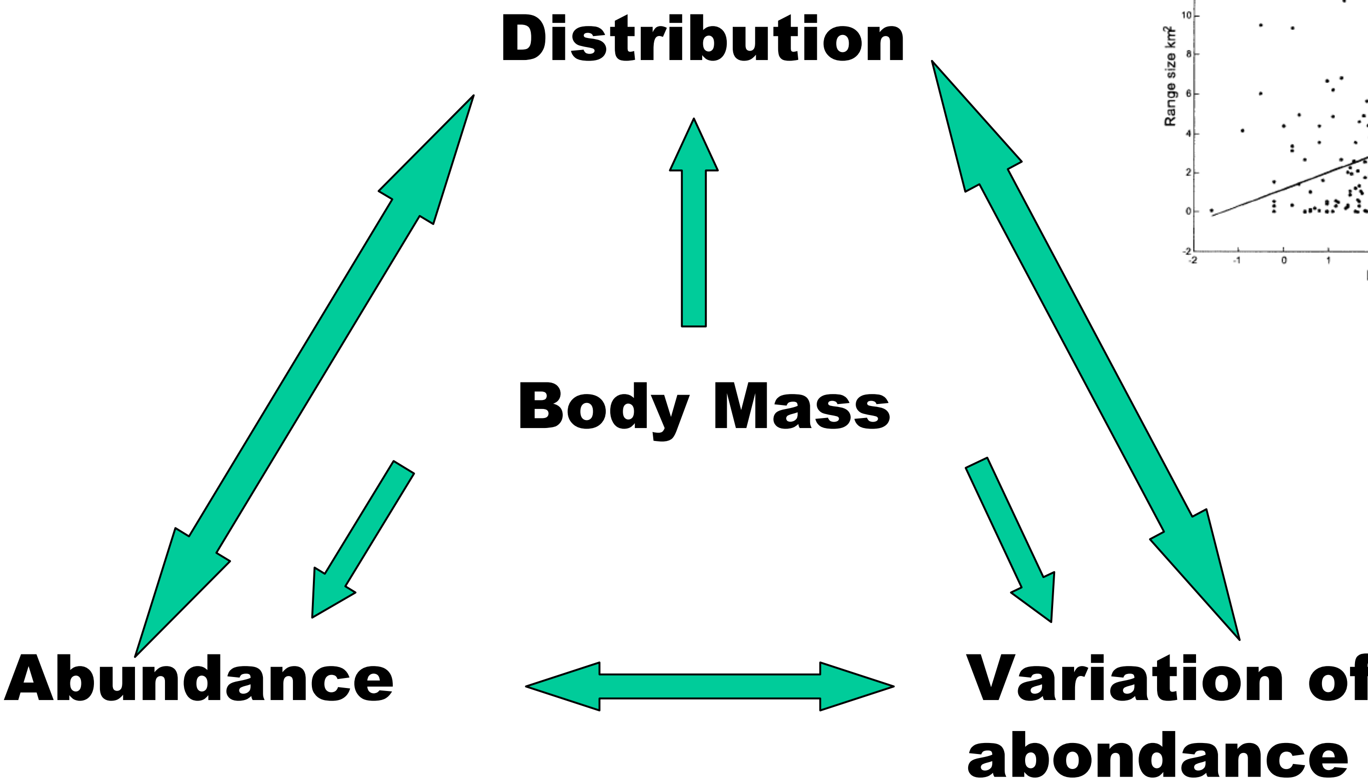

Comparative studies
Macroecology
Life History
Evolution

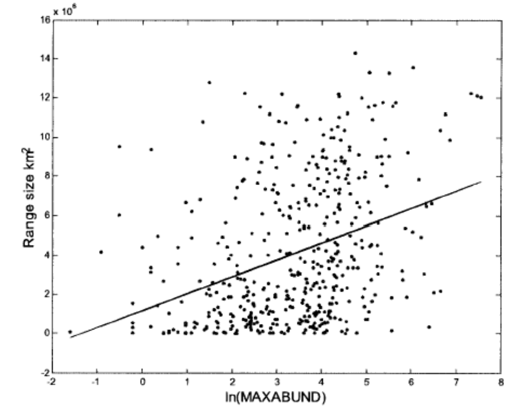
WHAT IS MACROECOLOGY ?

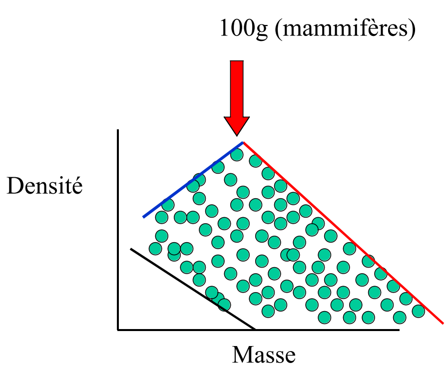
Distribution and Abundance of species at large spatial and temporal scales (Brown, 1995)

Some questions:

- Why some communities are species-richer than others?
- What are the determinants, what are the correlations ?
- What are the causes (“process”) of these observations (“patterns”)

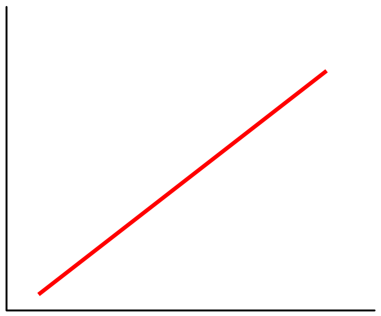

Distribution
Body Mass
Abundance
Variation of abondance


x 10^6
Range size km^2
ln(MAXABUND)

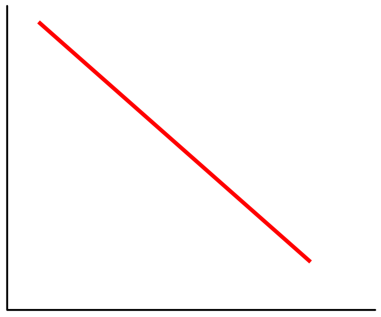

100g (mammifères)
Densité
Masse

LIFE HISTORY EVOLUTION

- Allometry rule



- Trade-offs



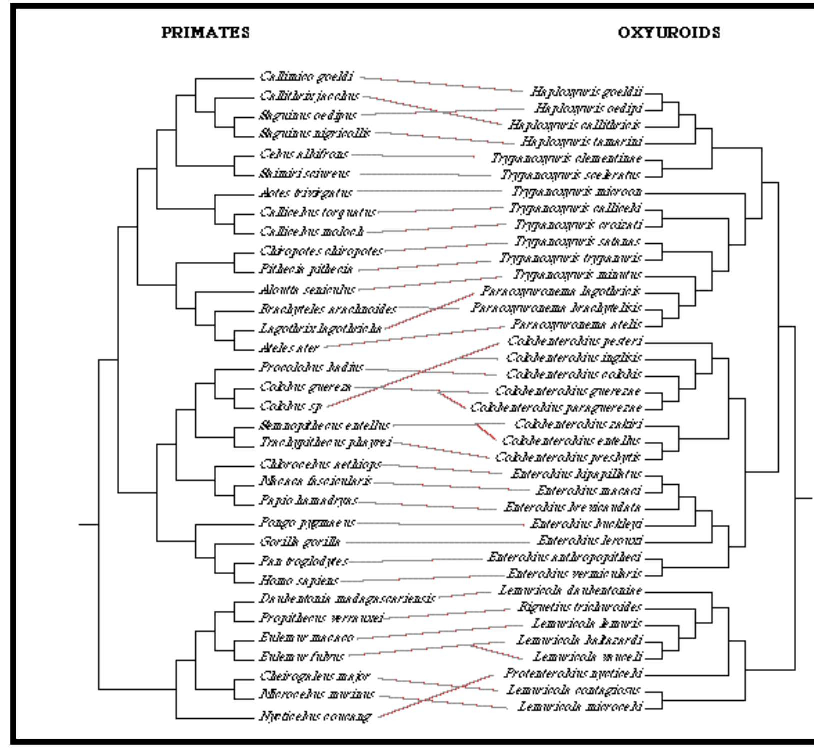
- Life history invariants

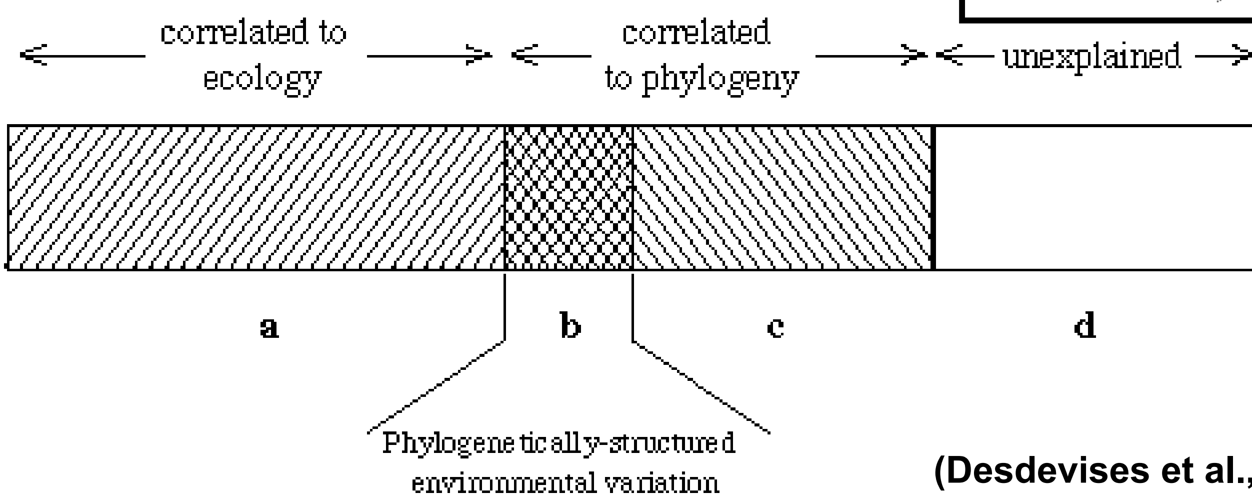
The importance of history, i.e. phylogenies

- ancestral states reconstruction

- comparative analyses
  - co-speciation
  - evolution of traits
  - key of innovation...

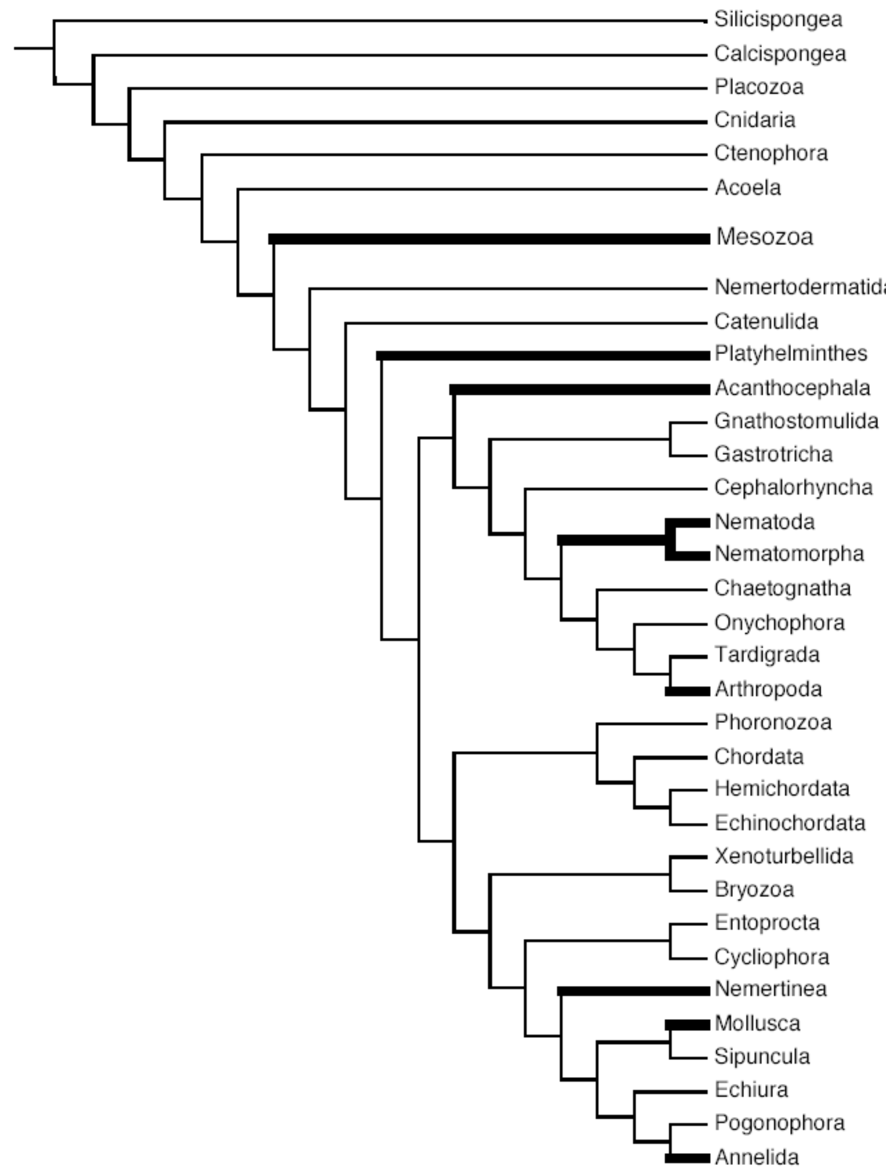
- phylogenetic inertia





(Desdevises et al., 2003, Morand & Poulin, 2003)

Why so many species of parasites?



1,000,000 described eucaryote species

100,000 parasite species

>70 transitions free-living parasites

(Poulin & Morand, 2004)

Nematodes as a model

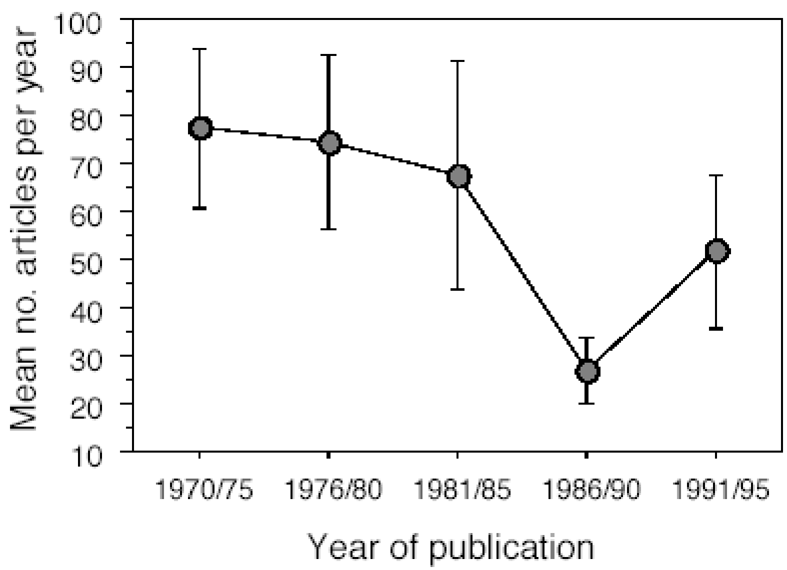
- morphological homogeneity
- free-living & parasites
- the use of epidemiological theory

Species diversity of nematodes

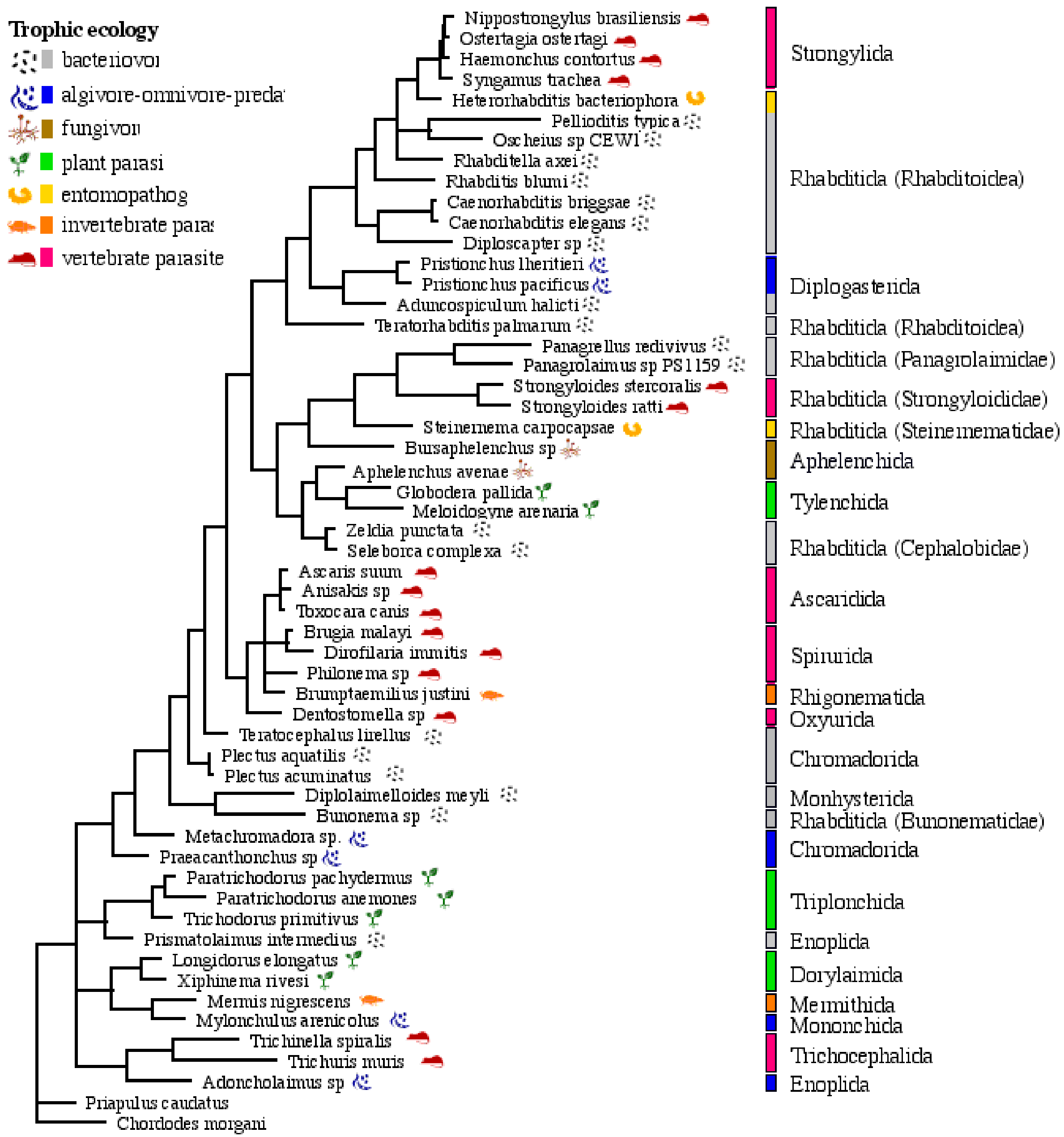
26,000 described species

1, 000, 000? (May, 1988)

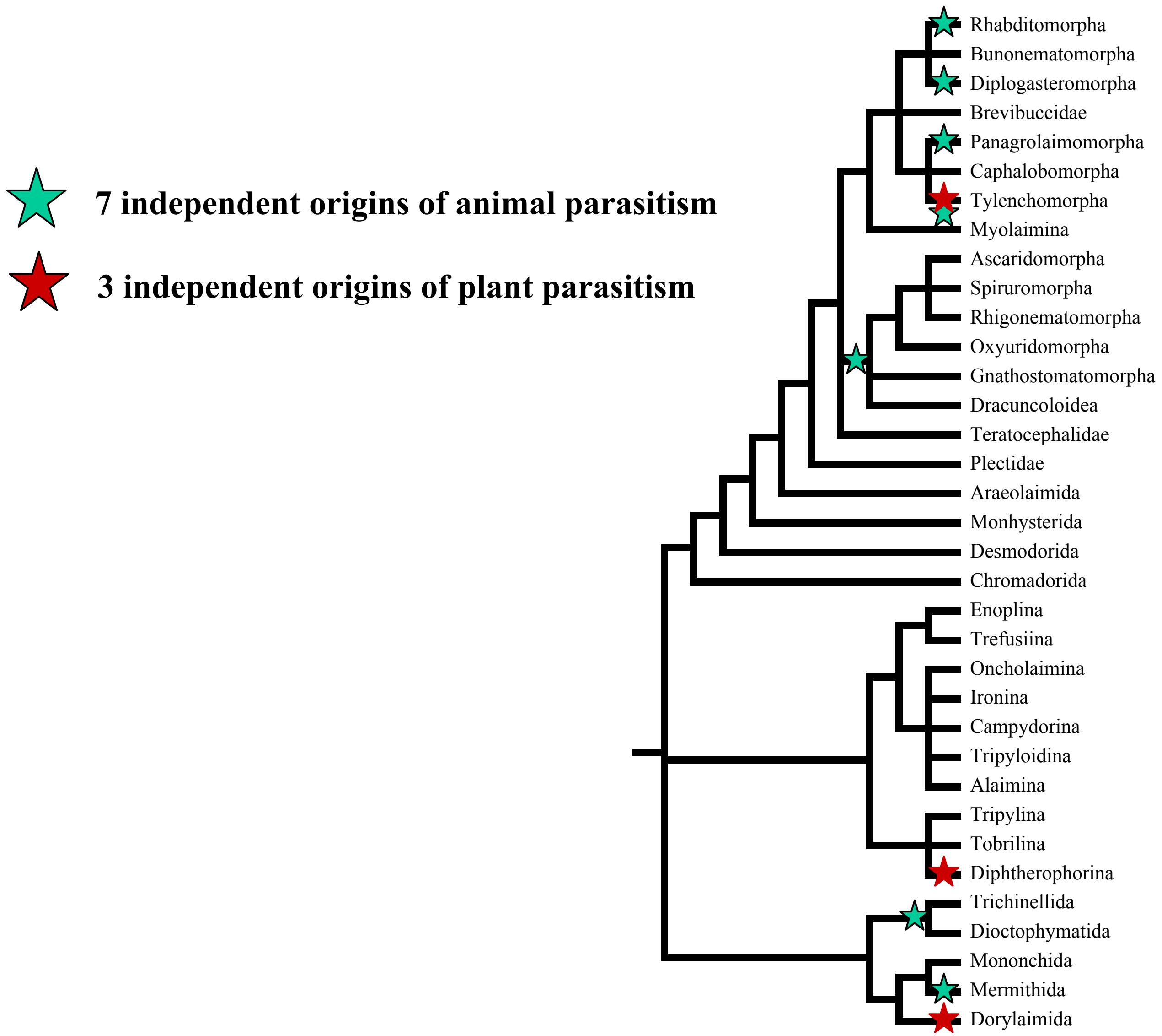
Mean number of Taxonomic papers



(Hugot, Beaujard & Morand, 2001)



(Blaxter et al., 1998)



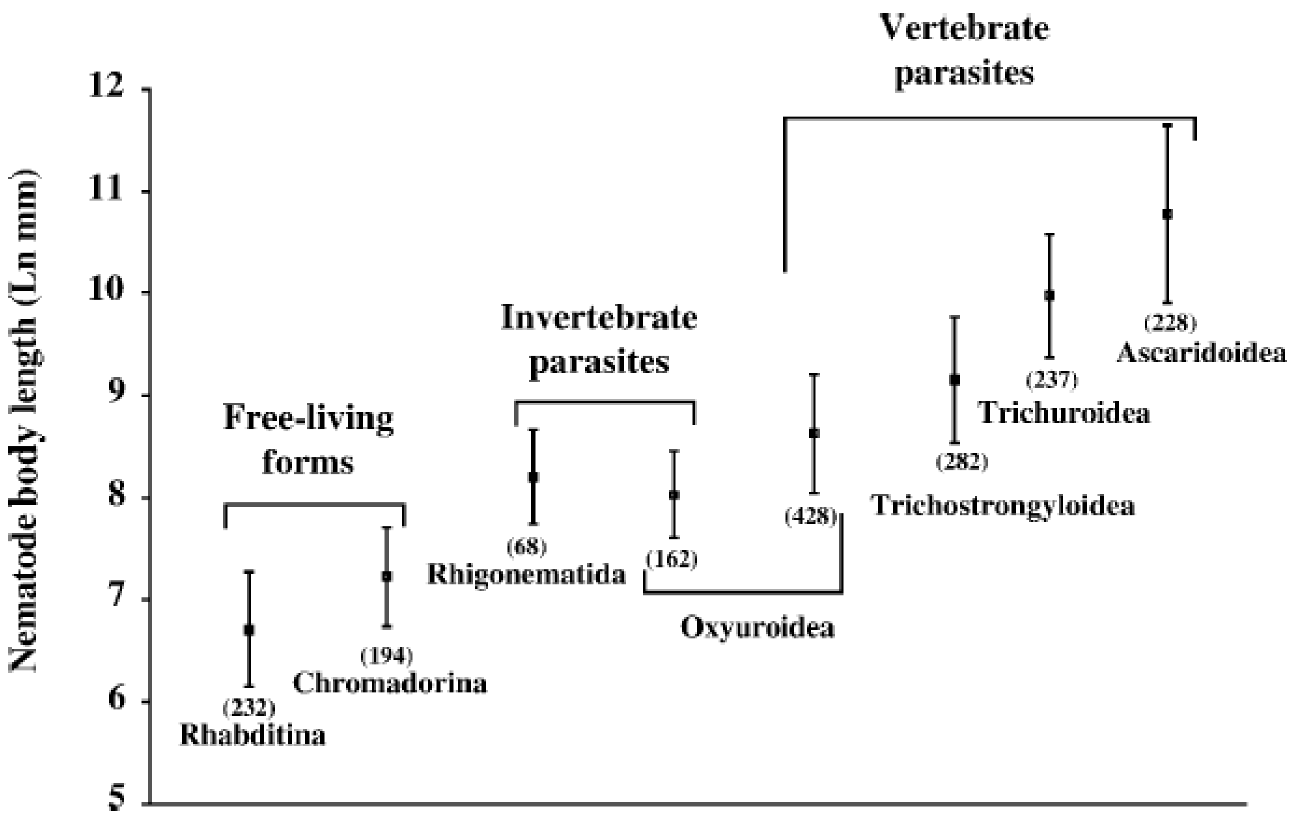
(Blaxter, 2003)

Life Styles	Species number	
Free-living marine	4070	
Free-living terrestrial	6610	
		10680
Plant parasites	4110	
Parasites of invertebrates	3500	
Parasites of vertebrates	8360	
		15860
Total species	26650	

(Hugot, Beaujard & Morand, 2001)

A first pattern

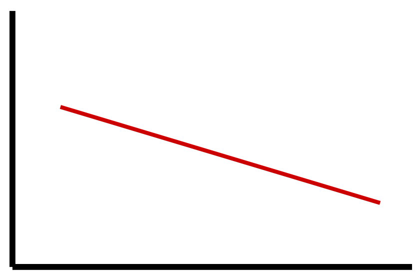
Changes in body size in relation to transition toward parasitism in nematodes



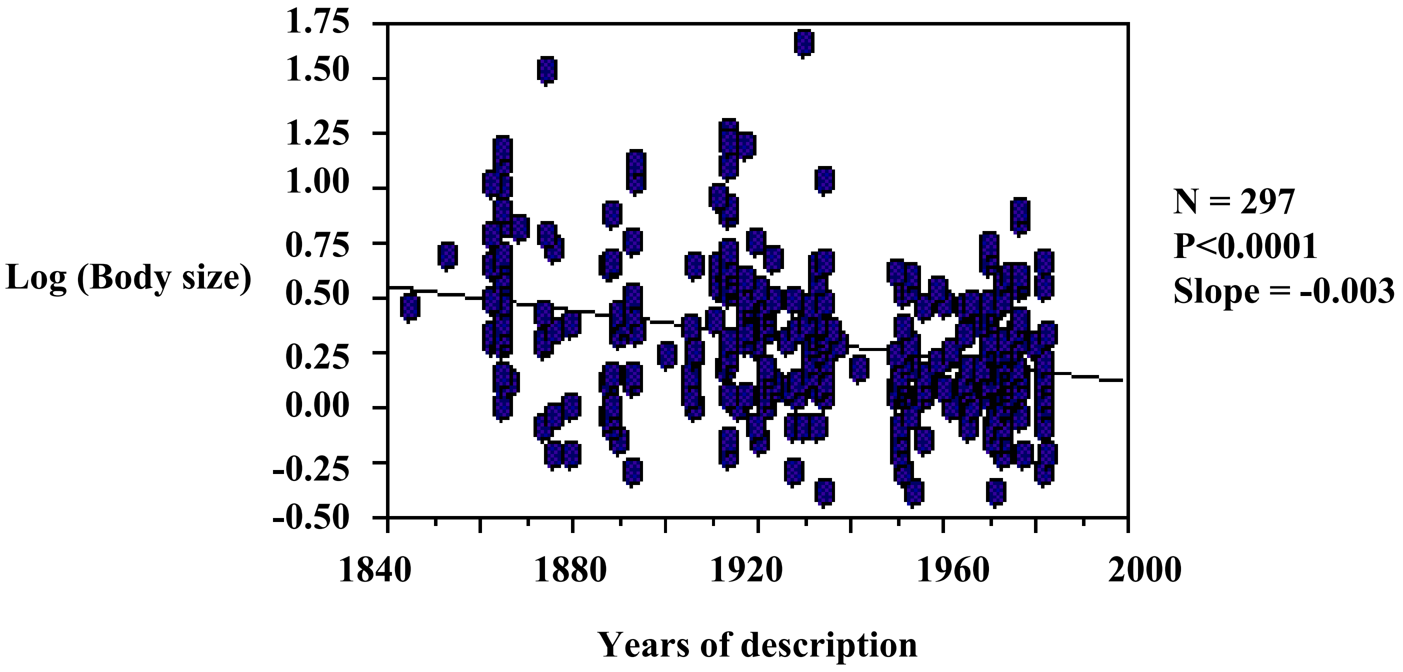
How to know that we have a good knowledge of the species diversity ?

Plot the body size vs the year of description (description starts with large-bodied species)

- 
  Small species remain to be described

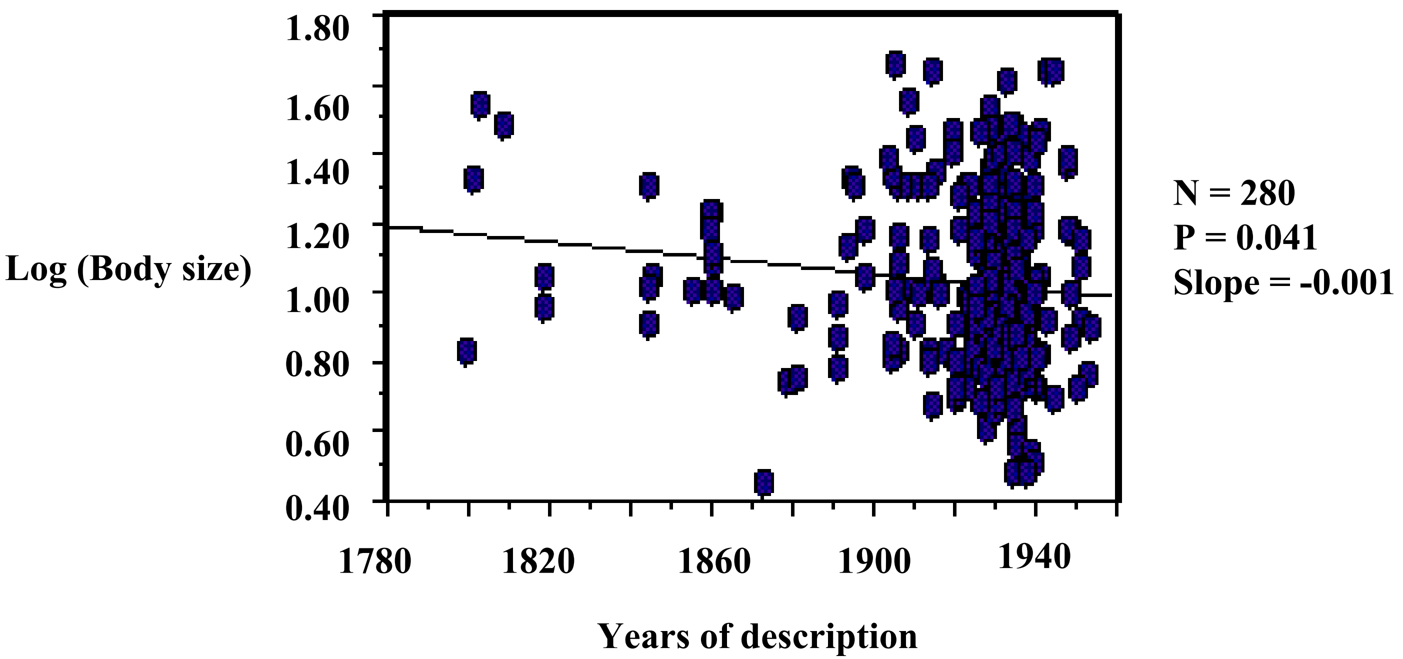
- 
  Small species described

Free-living nematodes (marine nematodes)

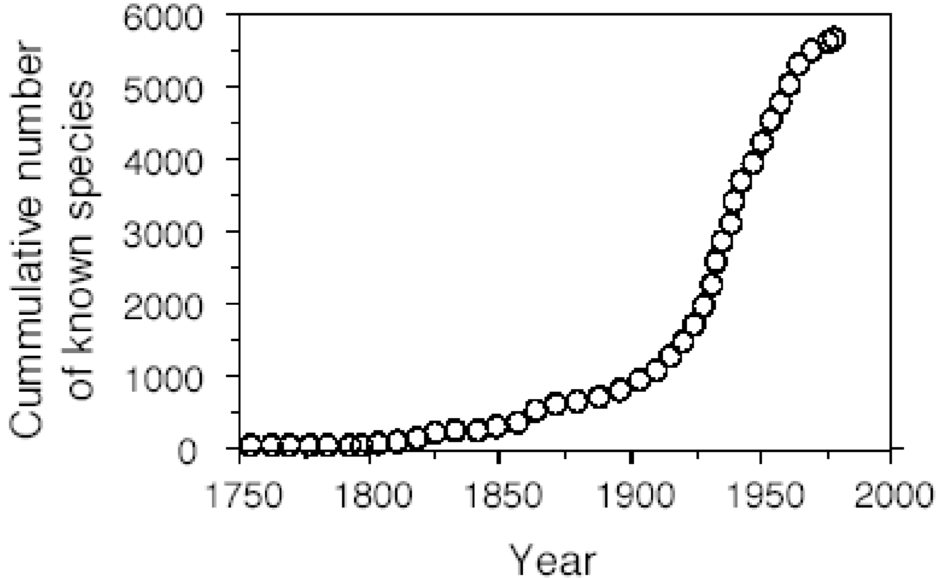


Good knowledge of the diversity

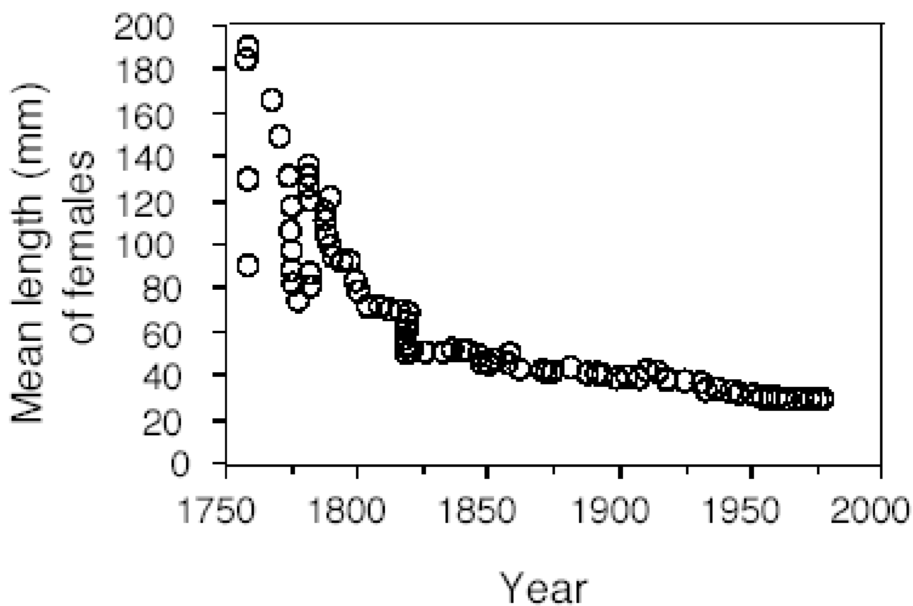
parasitic nematodes (Trichostrongylidae)



Bad knowledge of the diversity



No saturation, species number?



Good estimation of body size diversity

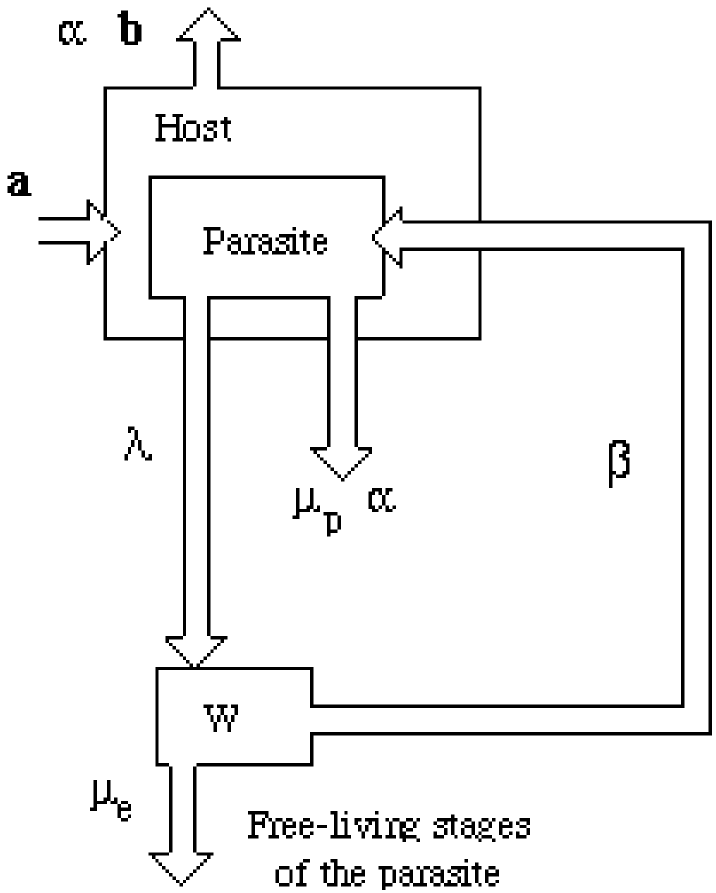
(Poulin & Morand, 2004)

First conclusion :

bad estimation of the diversity

good estimation of the morphological disparity

The role of mathematical models

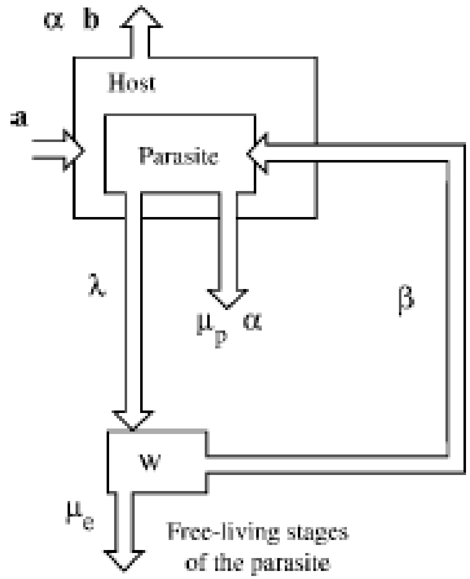


Differential equations

$$\frac{dH}{dt} = (a-b)H - \alpha P$$

$$\frac{dP}{dt} = \frac{\lambda \beta H P}{(\mu_e + \beta H)} - P\left(b + \alpha + \mu_p + \frac{k \alpha P}{(k+1)}\right)$$

THE BASIC TRANSMISSION RATE



R_0 is defined a the average number of new infection cases that arise from one infectious host, if introduced into a population of susceptibles

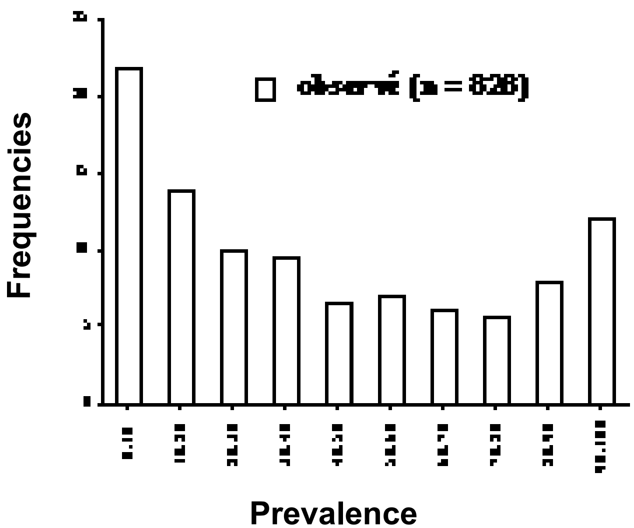
$$R_0 = \frac{\lambda \beta H}{(\mu_e + \beta H)(\alpha + \mu_p + b)}$$

- **transmission factor** → β
- **parasite fecundity** → λ
- **host density** → H
- **free-living stage (W) mortality** → μ_e
- **parasite virulence** → α
- **adult parasite mortality** → μ_p
- **host mortality** → b

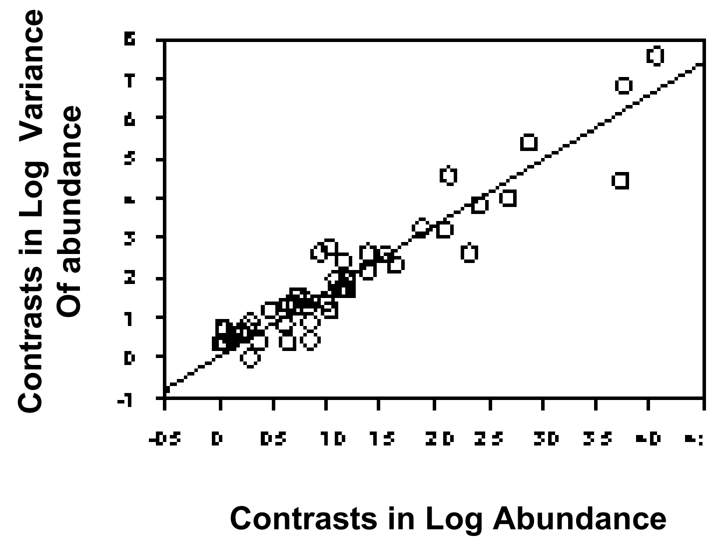
Do epidemiological models explain the pattern of abundance and distribution of parasitic nematodes?

TWO PATTERNS

Bimodal distribution of prevalence ("core-satellite" hypothesis)



A relationship between the variance of abundance and the abundance (Taylor's law)



Epidemiological processes ?

Prevalence (P) is linked to the abundance M :

$$P = 1 -[1 + M/k]-k$$

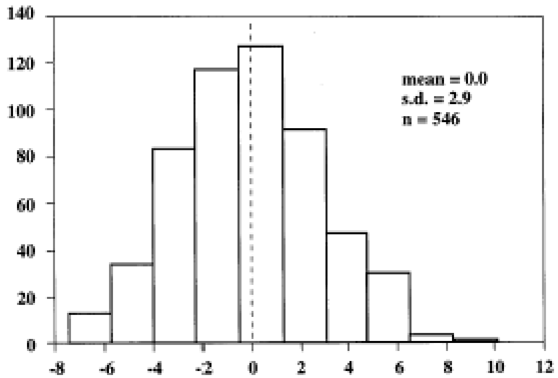
where k is the parameter of the Negative Binomial law, k is given by:

$$1/k = a\ M^{b}-2\ -1/M$$

The parameters a and b are given by the Taylors' power law, with V(M) the variance of abundance :

$$Log(V(M)) = b\ Log(M) + a$$

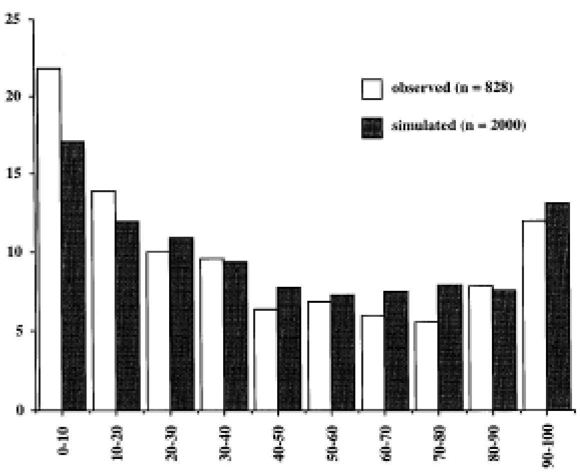
Simulation test and comparative analyses



Abundance follows a Log normal distribution

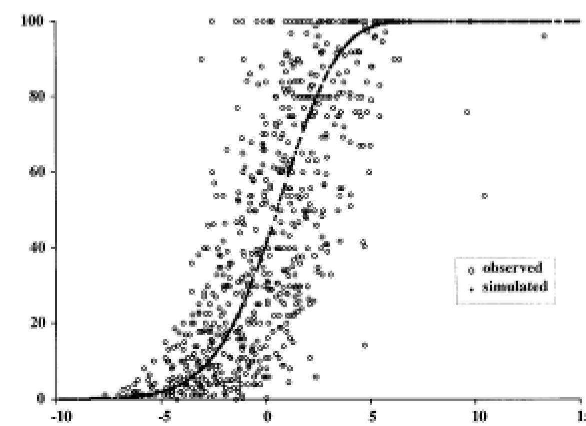
Simulation of M (0, 2.9)

k , V(m), P



Prevalence

Prevalence

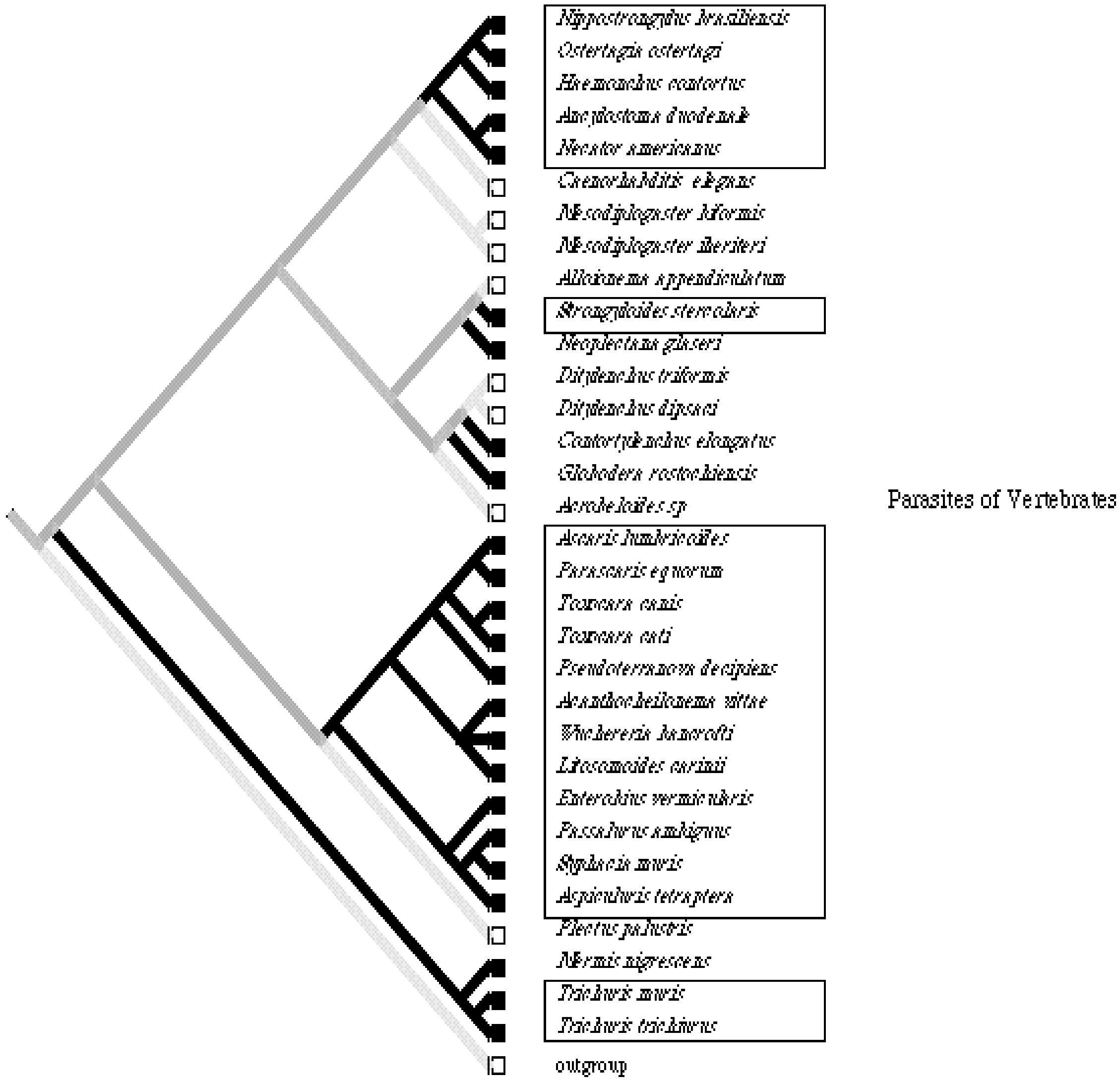


Abundance (M)

Second conclusion :

simple epidemiological model describes well the distribution (prevalence) and abundance of nematodes (at least for vertebrate nematodes)

Evolution
of
Nematode Life traits

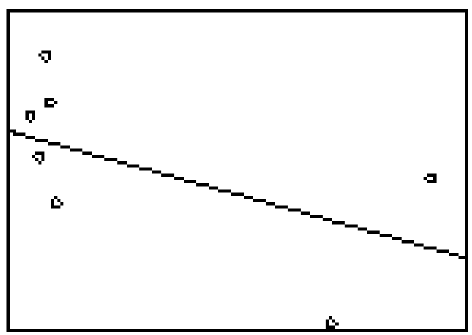


transition toward parasitism
-> increase in size
-> increase in fecundity

Phylogeny: Blaxter et al. 1998. Nature 392: 71-75

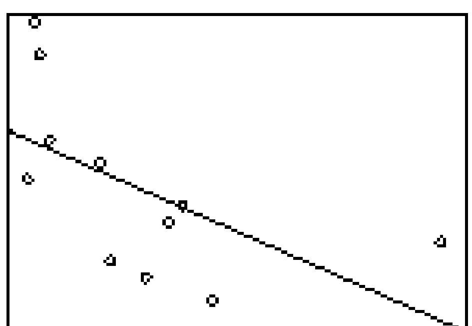
These relationships are independent of life style (parasite *vs* free-living)

Life span of free-living stages

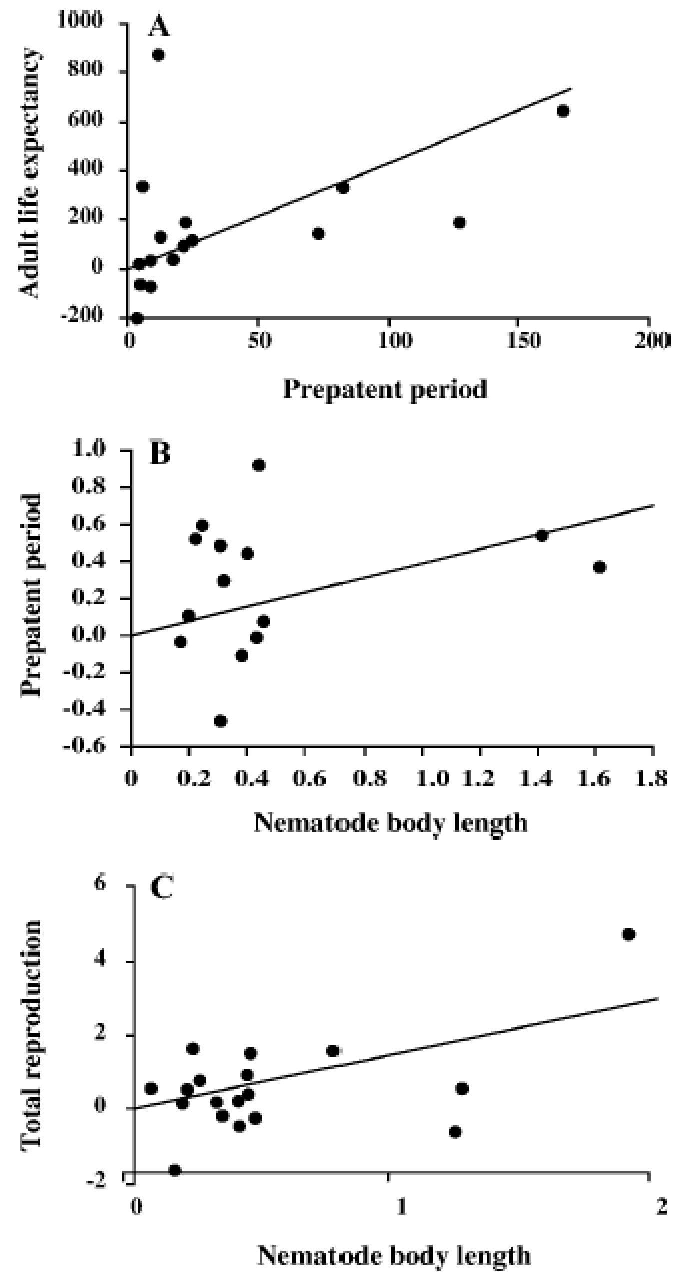


Contrasts in Fecundity

Life span of adult stages



Contrasts in Fecundity

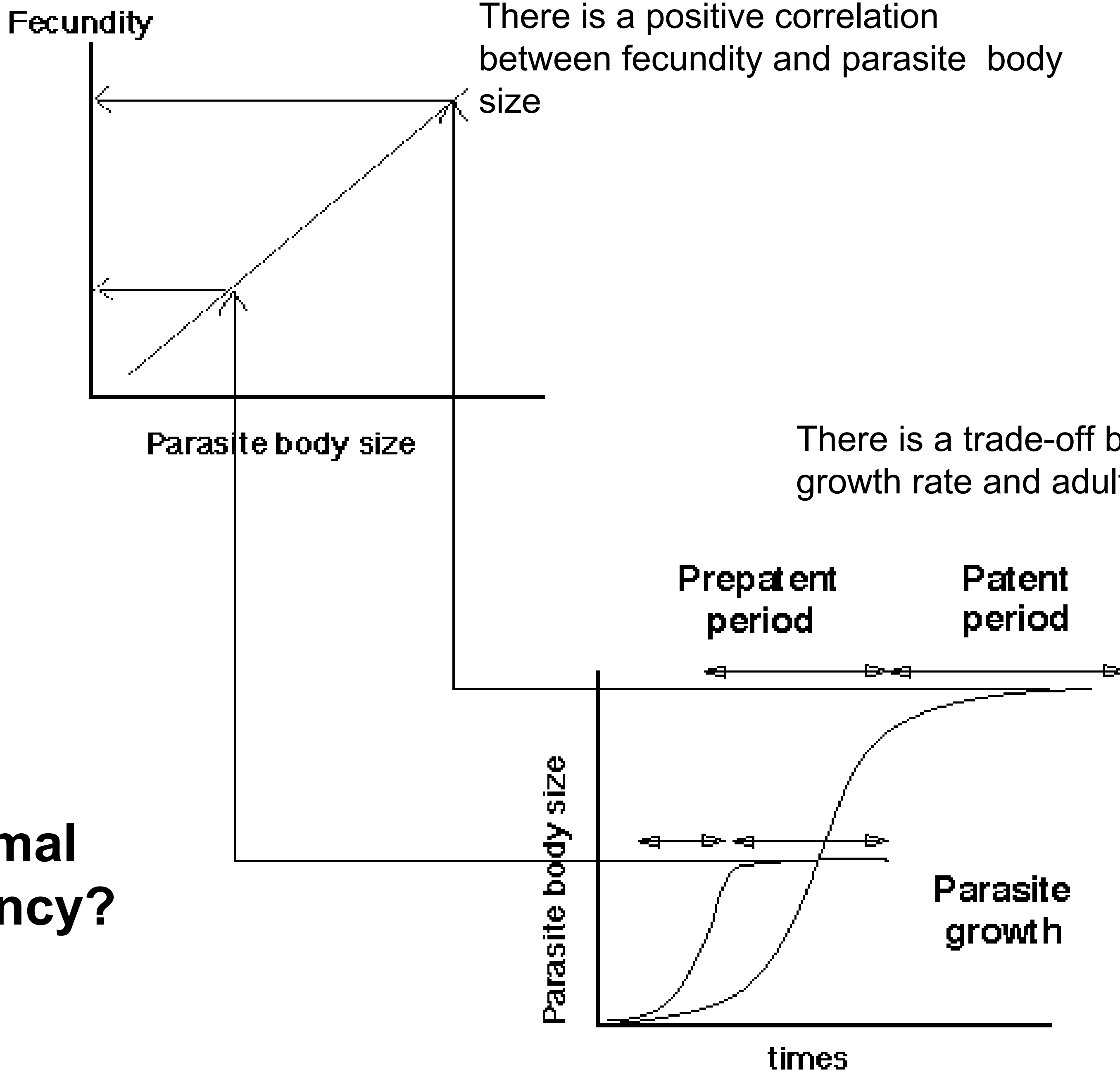


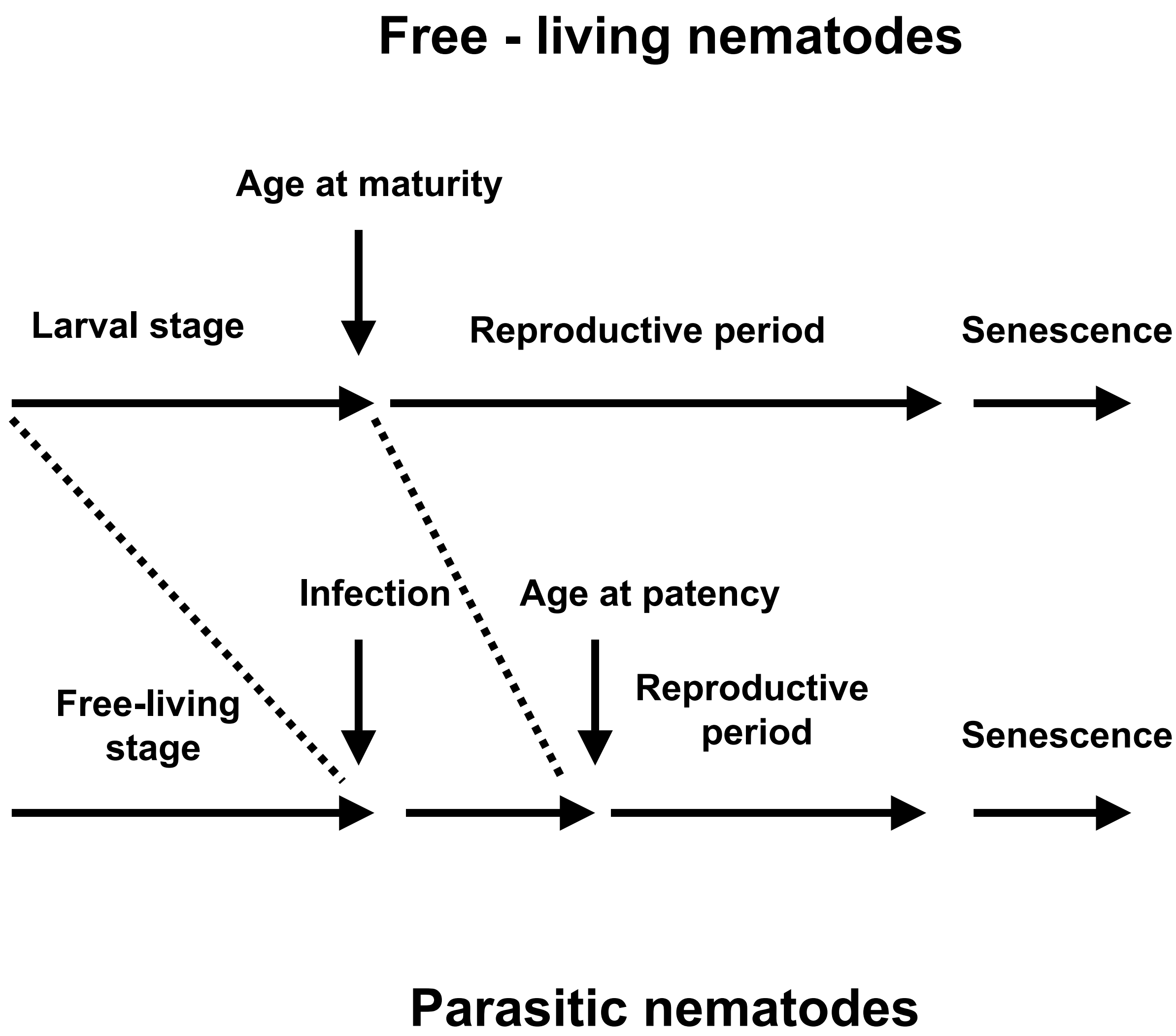
(Morand, 1996)

Optimal Patency?

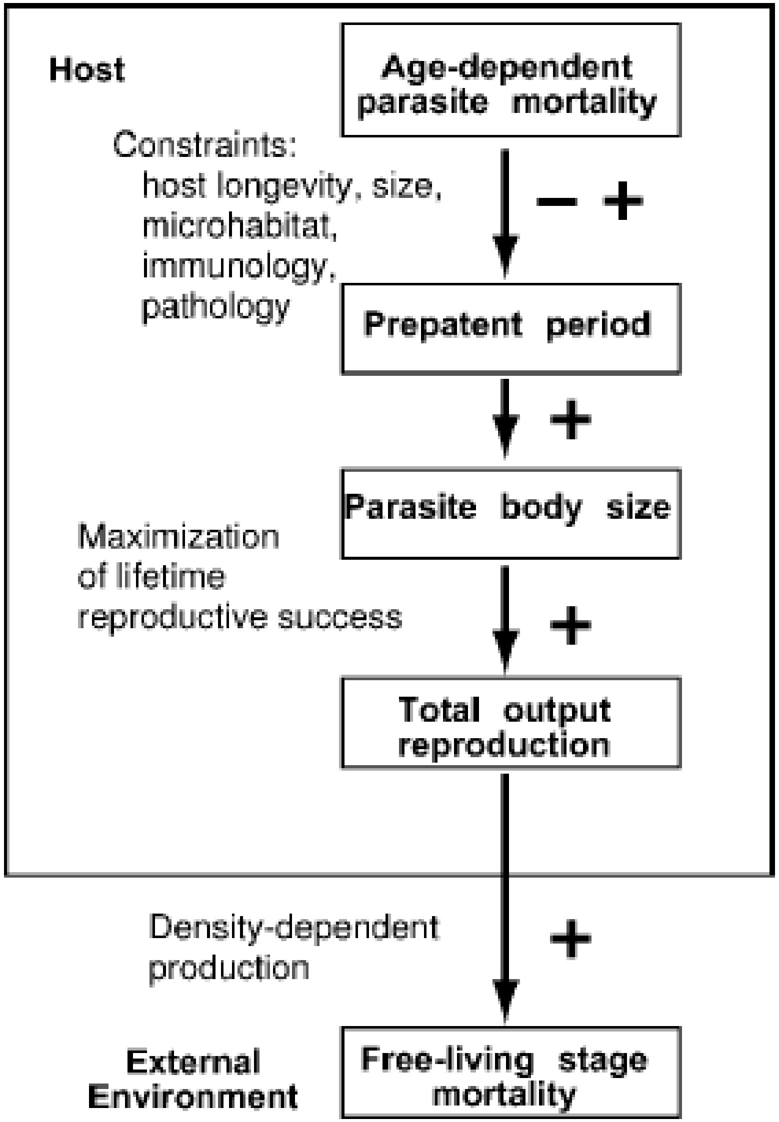
There is a positive correlation between fecundity and parasite body size

There is a trade-off between growth rate and adult size



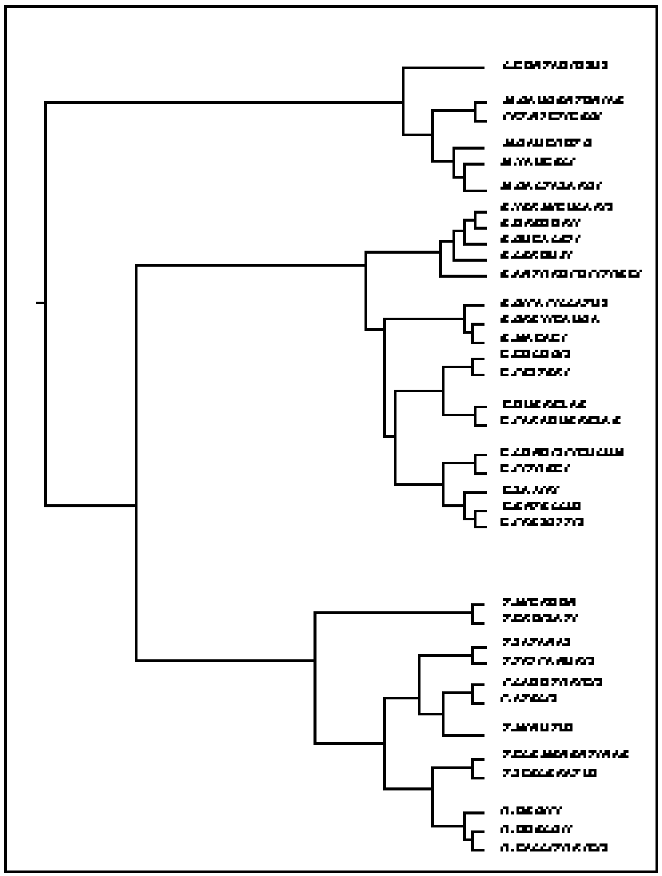

Free - living nematodes
Age at maturity
Larval stage
Reproductive period
Senescence
Infection
Age at patency
Free-living
stage
Reproductive
period
Senescence
Parasitic nematodes

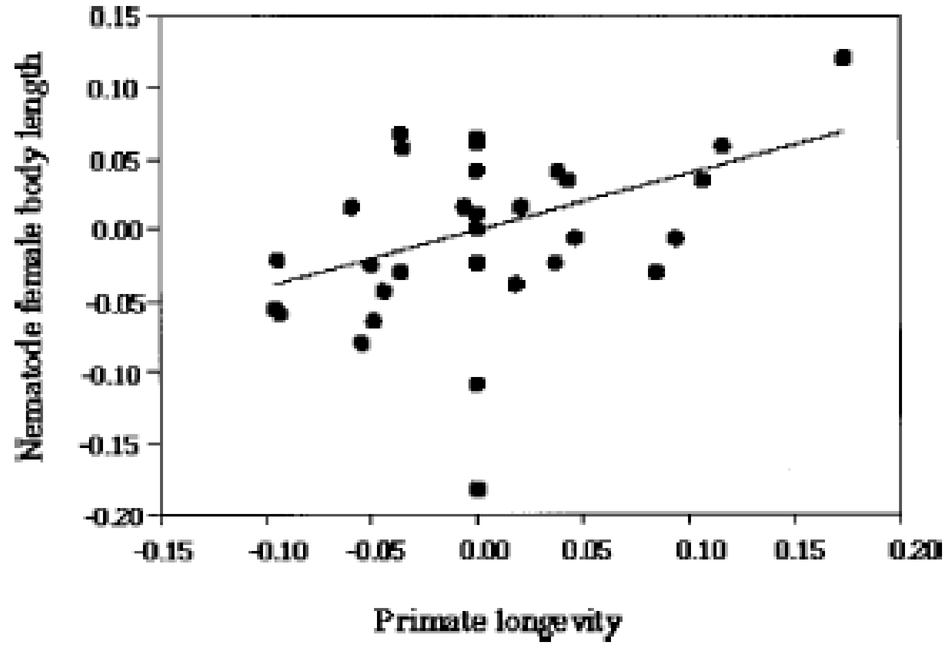
A causal chain



(Morand, 1996)

A first comparative test





Oxyures of Primates

(Sorci & Morand, 1998; Sorci, Morand & Hugot, 1998)

Third conclusion :

• living styles (parasitic vs free-living) do not influence the evolution of life traits

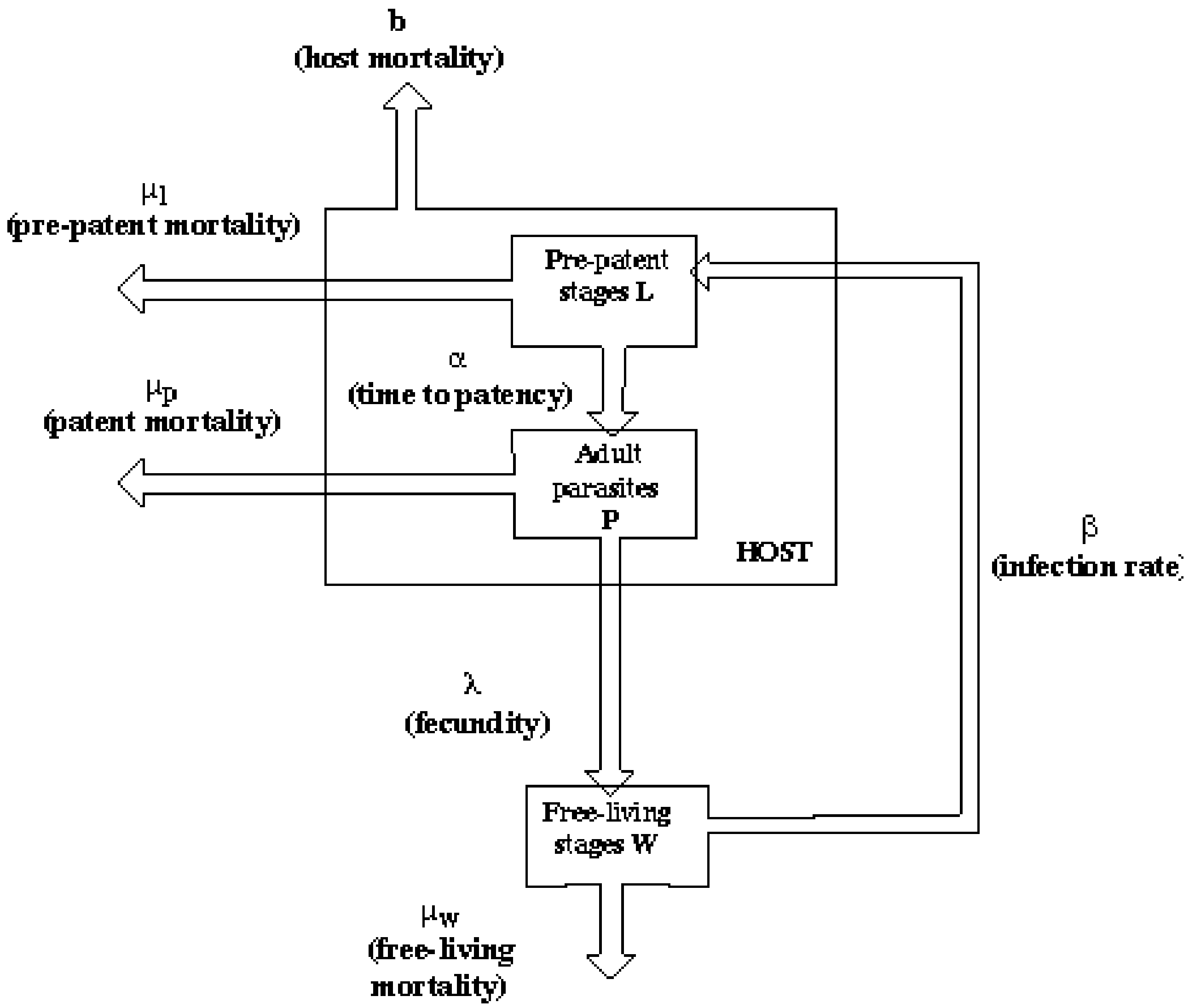
• adult mortality drives the evolution of life traits trough the age at maturity (patency for parasites)

Optimal Age at Maturity
(optimal patency)

- theoretical predictions

- comparative test

A model



(Morand & Poulin, 2000)

The Equations

The larval population dynamics (L)

$$\frac{dL}{dt} = \frac{\lambda \beta H P}{(\mu_w + \beta H)} - \frac{L}{\alpha} - (b + \mu_L)L$$

The adult parasite population dynamics (P)

$$\frac{dP}{dt} = \frac{L}{\alpha} - (b + \mu_p)P$$

The basic transmission rate

The expression of the basic transmission rate is obtained by considering the increase of the parasite population when one parasite is introduced in a population of uninfected hosts (see Anderson & May, 1985 for derivation)

$$R_0 = \frac{\lambda \beta H}{\alpha(\mu_w + \beta H)\left(\frac{1}{\alpha} + b + \mu_L\right)(b + \mu_P)}$$

The basic transmission rate can be used as a fitness measure of a mutant parasite, assuming that multiple infections do not occur

The parasite fitness is maximal if its time to patency is optimal. The optimal time to patency is obtained by solving

$$\frac{d R_0}{d\alpha} = 0$$

Incorporating empirical relationship between the time to patency and the length of the adult worm and the relationship between the fecundity and the length (Morand, 1996), this gives :

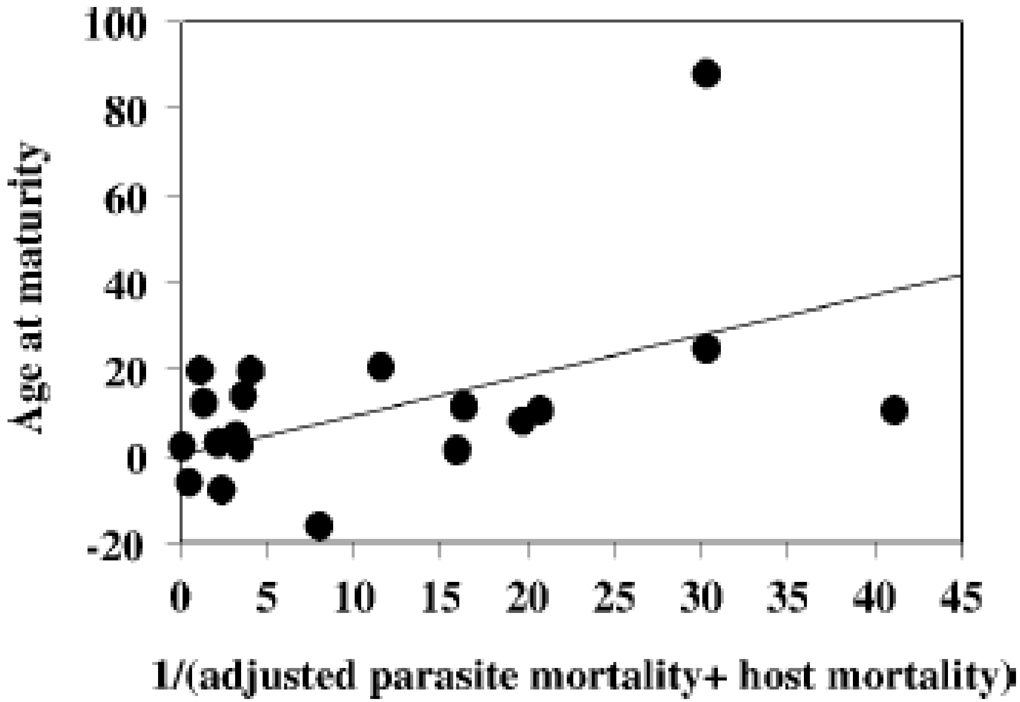
$$\frac{\left(\alpha^{a}\right)^{c}\mu_{P}\beta H\left(ca\,\mu_{L}\alpha + ca + cab\alpha - \mu_{L}\alpha - b\alpha\right)}{\alpha\left(\mu_{w} + \beta H\right)\left(\mu_{L}\alpha + 1 + b\alpha\right)^{2}\left(\mu_{p} + b\right)} = 0$$

Using estimated values of c (1.89 ± 0.31) and a (0.39 ± 0.15), and independent contrasts on data, gives the optimal time to patency

$$\alpha^* = \frac{2.80}{\mu_L + b} \qquad \left[\frac{0.63}{\mu_L + b}, \frac{90}{\mu_L + b}\right]$$

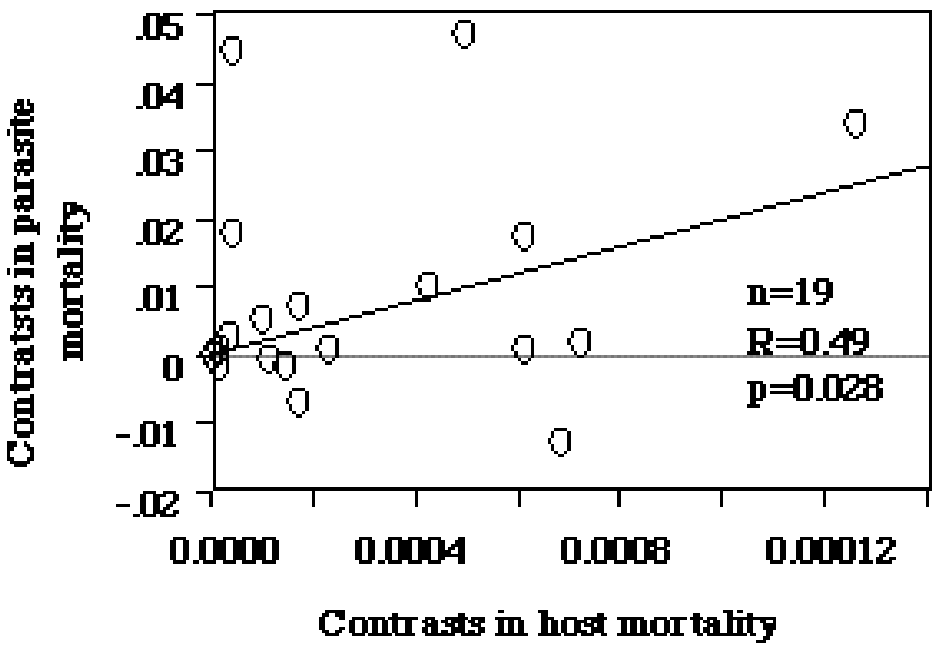
Which depends on both larval parasite mortality and host mortality (b)

According to the prediction, the optimal age at maturity, i.e. optimal patency, is dependent from host mortality



Slope = 0.93 (sd 0.26)

Co-variation in mortality

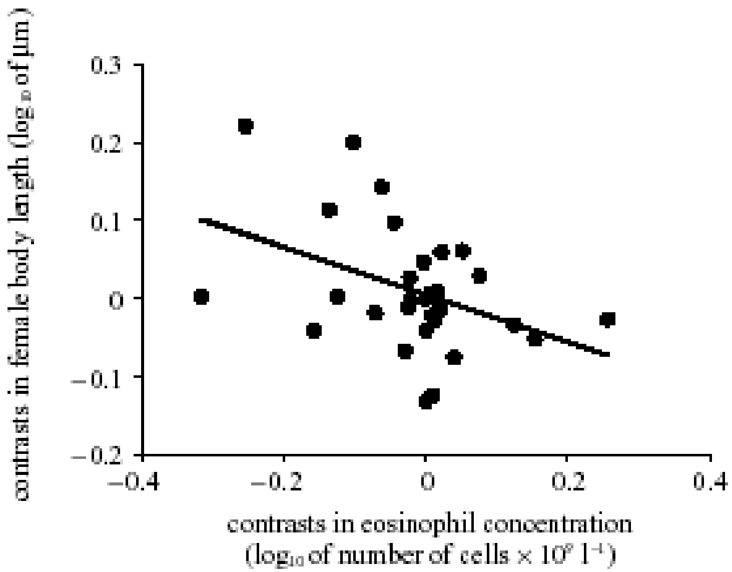


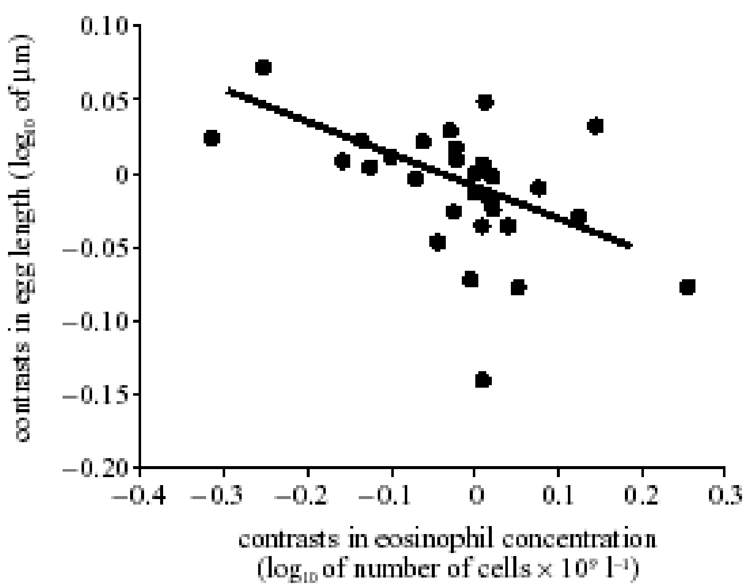
Fourth conclusion :

- **epidemiological model explains the pattern of life traits**

- **epidemiological processes at the basis of life-traits evolution**

Host immunity and nematode life traits : the case of primates and pinworms





Increased investment in immunity favours small bodied size nematodes (and small eggs)

(Sorci et al., 2004)

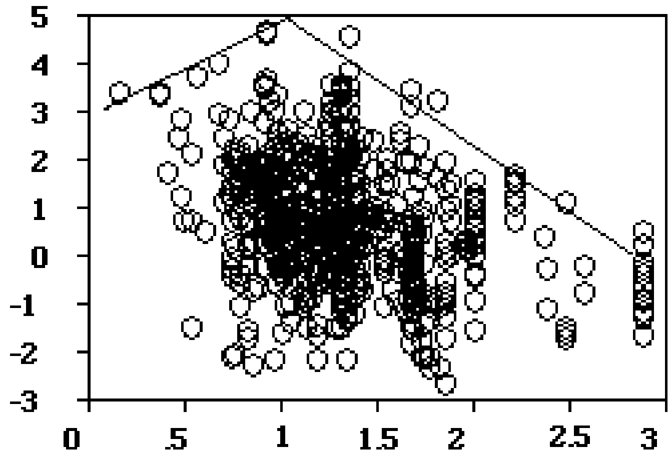
PATTERN OF NEMATODE BODY SIZE DISTRIBUTION

- theoretical predictions

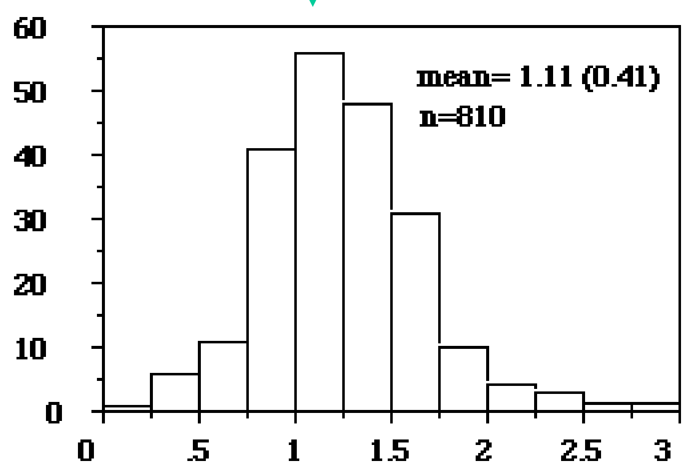
- comparative test

Two patterns

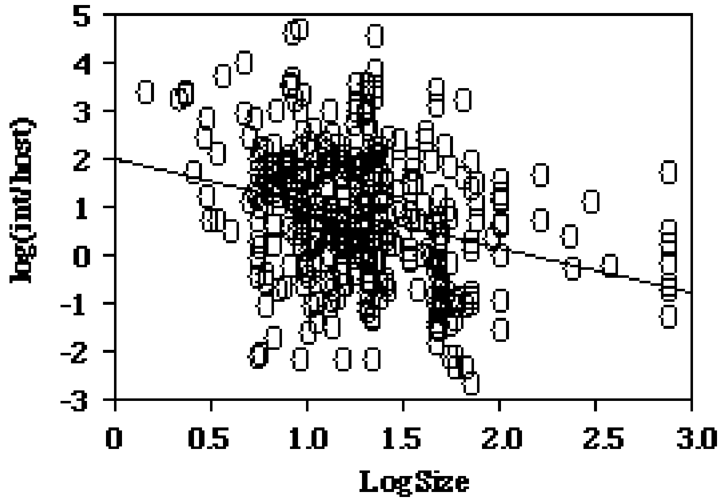
Nematode density



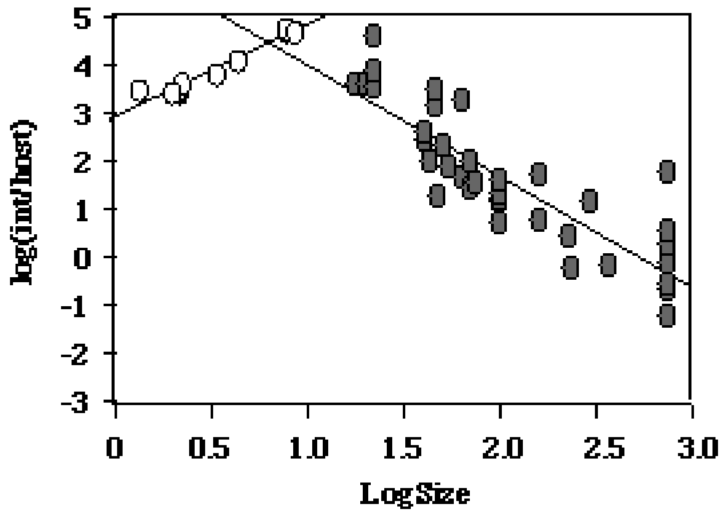
Species number



Nematode body size



Nematode density



slope sup= -2.318 (0.218)
n=340
R=0.865
$p<0.0001$

slope inf= 1.920 (0.247)
n=8
R=0.854
p=0.0002

Nematode body size

(Morand & Poulin, 2002)

Parasite population dynamics

$$\frac{dP}{dt} = \lambda\beta HP - \left(b + \mu + \left(\frac{(k+1)}{k}\right)P\right)P$$

Host population dynamics

$$\frac{dH}{dt} = aH - bH$$

The basic reproductive rate R_0 corresponds to the number of female offspring produced by an adult female worm throughout her reproductive lifespan, which survive to reach sexual maturity.

The value of is then derived from (Dietz, 1975)

$$\frac{1}{P}\frac{dP}{dt} > 0$$

This gives the following expression of the basic reproduction ratio

$$R_0 = \frac{\lambda\beta H}{(\mu + b)}$$

All these parameters are linked with body size, either host body size or parasite body size.

$$R_0 = \frac{\beta S_p^a W_H^{-0.75}}{\left(\left(S_p^a\right)^d + W_H^{-0.25}\right)}$$

The optimum parasite body size is obtained by solving

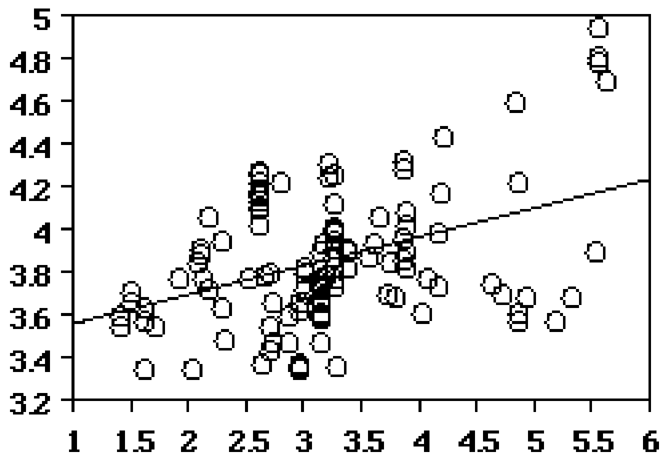
$$\frac{\delta R_0}{\delta S_P} = 0$$

This allows the following optimal parasite body size

$$S_p^* = e^{\left(-\frac{\ln\left(1/\left(W_H^{0.25}\right)(1+d)\right)}{da}\right)}$$

log(Sp* in mm)= 0.38 log(Host body size in g)

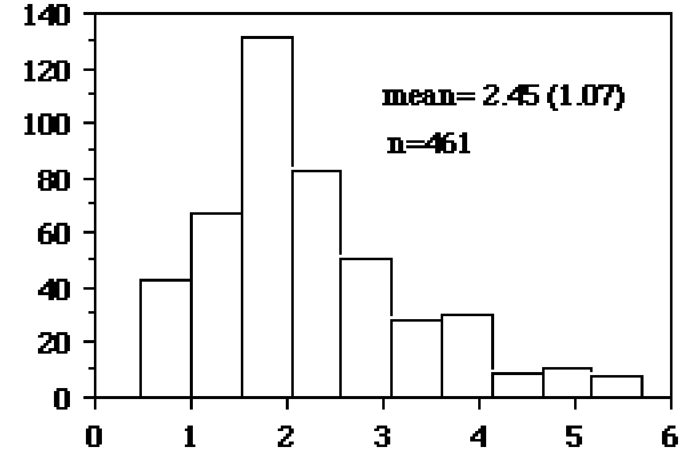
Observed co-variation in body sizes



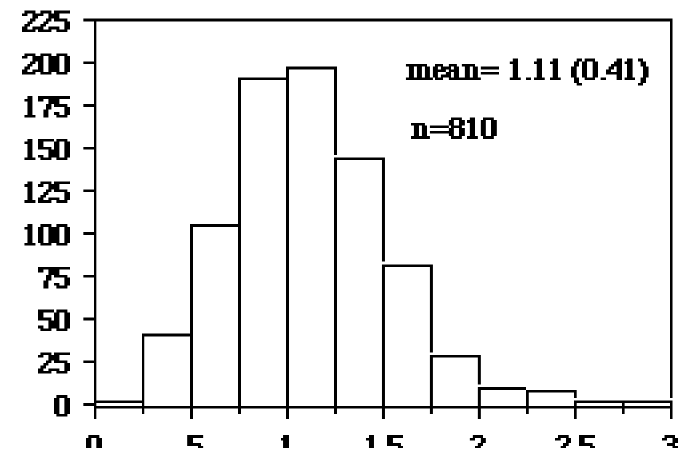
slope = 0.33 (0.28-0.39)
n= 115
R= 0.41
p<0.0001

Predicted slope : 0.38

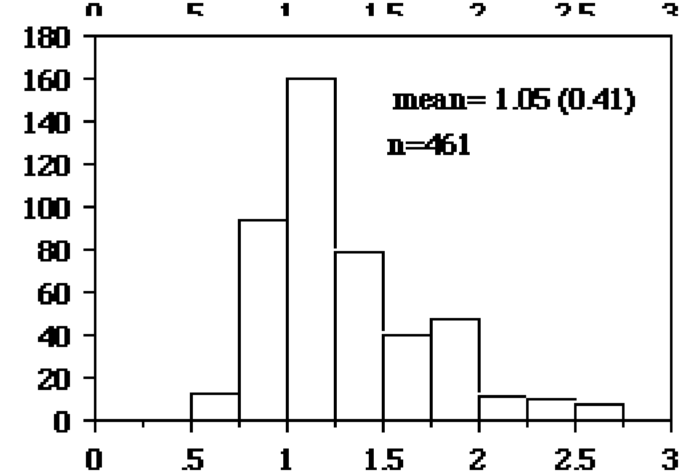
Observed distribution of mammal body mass



Observed distribution of nematode body size



Simulated distribution of nematode body size



General conclusion

Processes can be investigated using
- Life history theory
- Population dynamic theory

Theoretical predictions can be tested using
- Comparative analyses

Collaborators

Jean-François Guégan (IRD)
Jean-Pierre Hugot (MNHN Paris)
Robert Poulin (University of Dunedin)
Gabriele Sorci (Université Paris 6)