Self-organized processes in social insects

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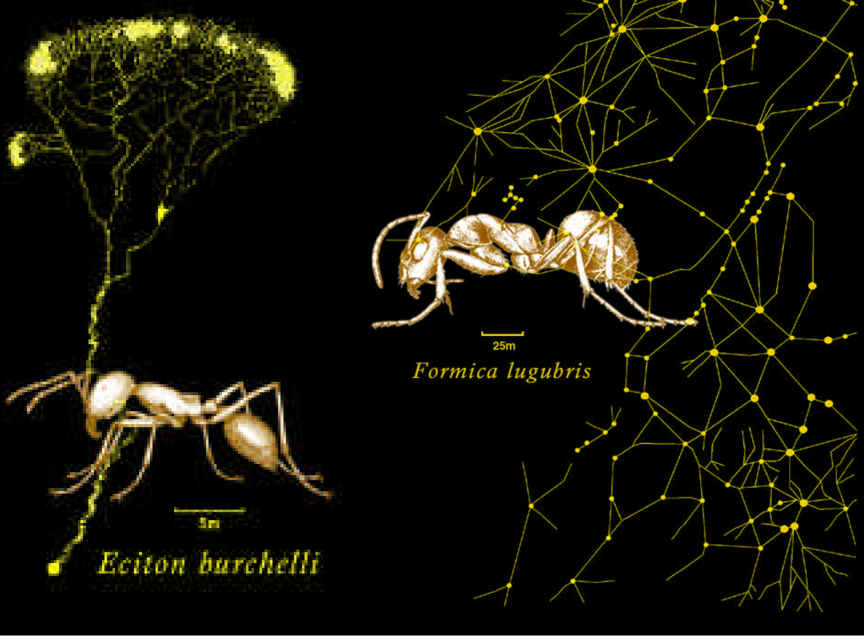
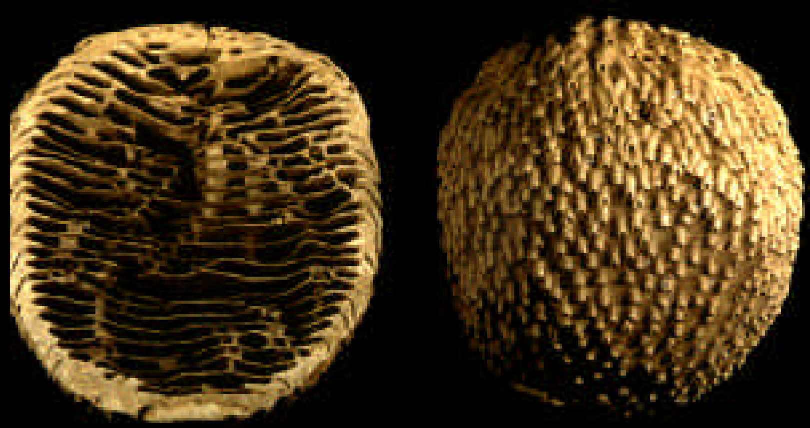
Large-scale networks



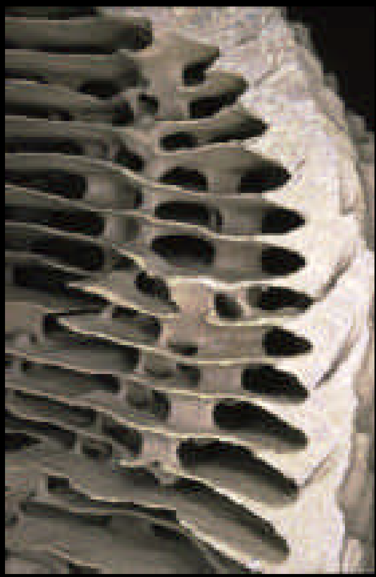
Large-scale structures

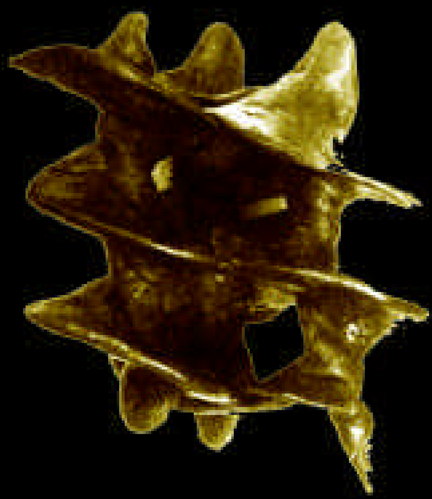
Complex structures



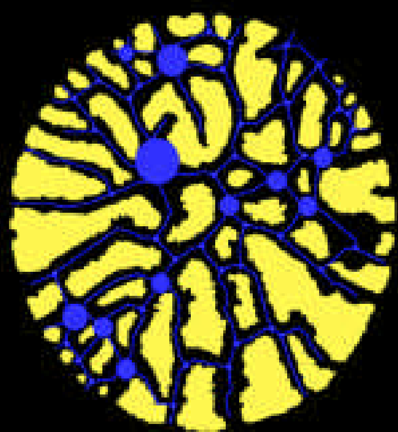
Apicotermes arquieri

Complex structures





Complex network structures



Subterranean galleries network in the ant *Messor sancta*

Complex network structures

real time: 3 days

A large number of actions

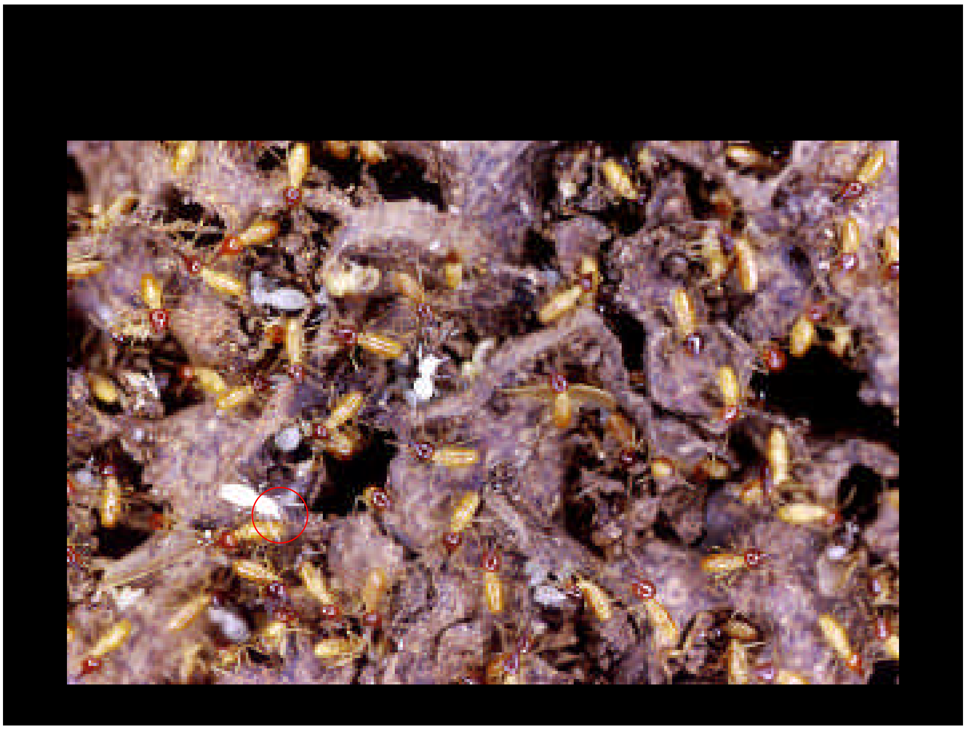
Dynamic patterns

Nest building in the ant *Lasius niger*

real time: 2 days

Dynamic patterns

Evolution of the nest structure in the ant *Lasius niger*

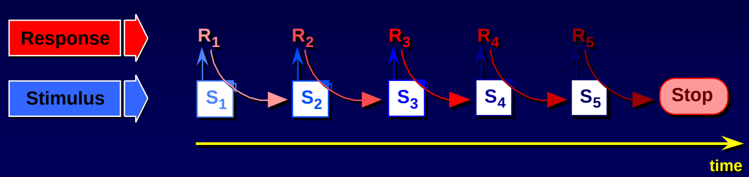


Pierre-Paul Grassé (1895-1985)

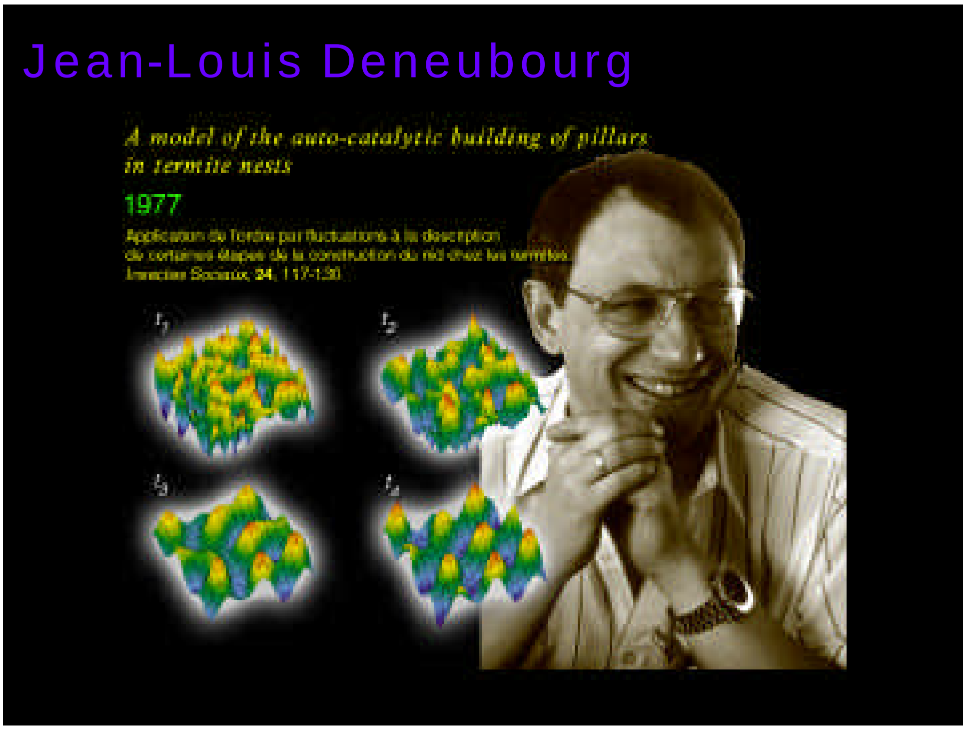
Stigmergy

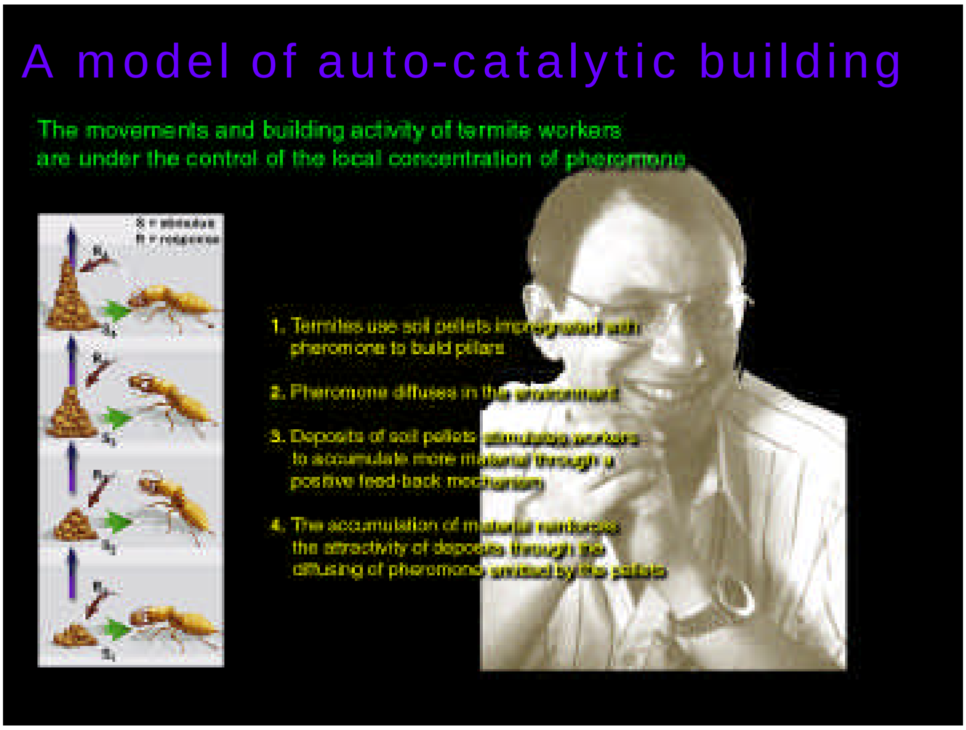
Simple rules, complex paterns

- Stigmergy refers to a class of mechanisms that mediate animal-animal interactions: insects coordinate and regulate their activity through indirect interactions



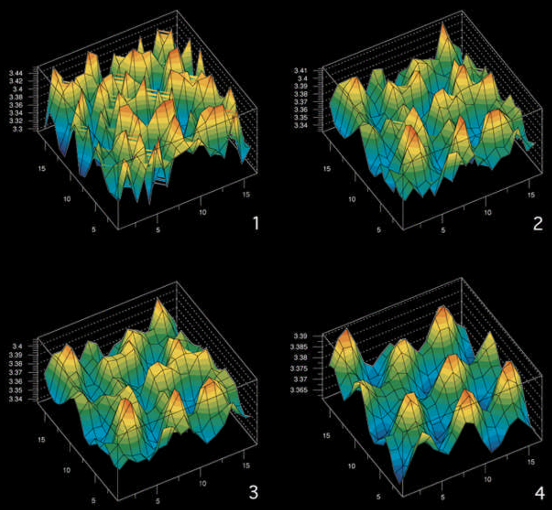
- When the stimulus-response sequence involves stimuli that differ quantitatively (such as pheromone fields and gradients), the probability of response of the individuals to these stimuli is modified


Jean-Louis Deneubourg
A model of the auto-catalytic building of pillars
in termite nests
1977
Application de l'ordre par fluctuations à la description
de certaines étapes de la construction du nid chez les termites
Insectes Sociaux, 24, 117-130


A model of auto-catalytic building
The movements and building activity of termite workers
are under the control of the local concentration of pheromone
1. Termites use soil pellets impregnated with pheromone to build pillars
2. Pheromone diffuses in the environment
3. Deposits of soil pellets stimulates workers to accumulate more material through a positive feed-back mechanism
4. The accumulation of material reinforces the attractivity of deposits through the diffusing of pheromone emitted by the pellets

A model of auto-catalytic building

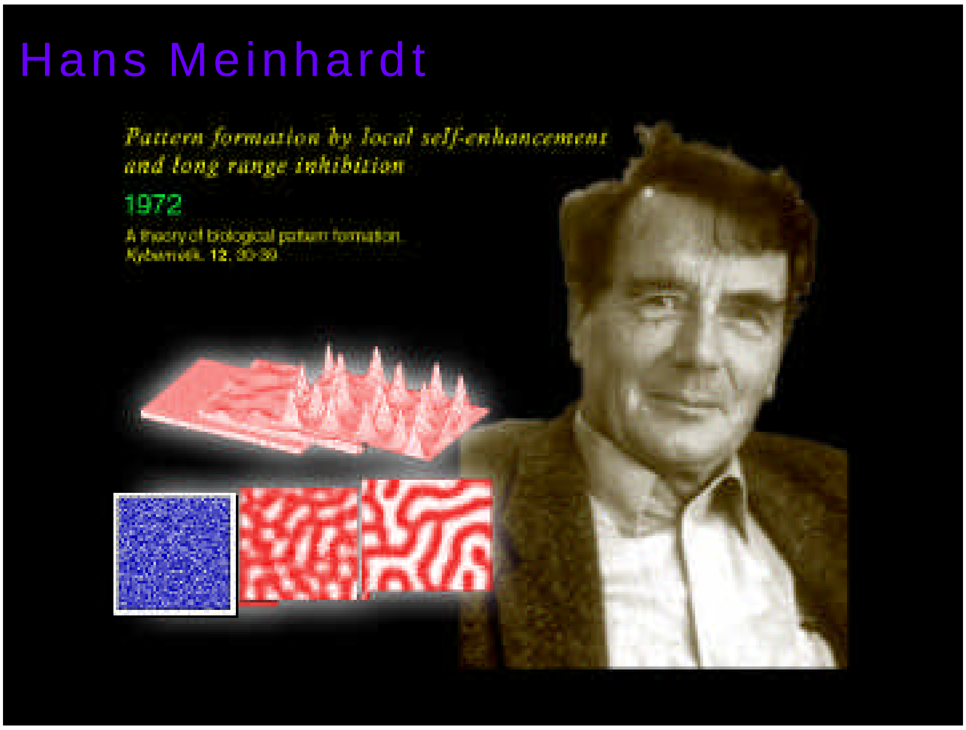
Four simulation steps showing the temporal evolution of the structure built by termites in a 2-D system



Stigmergy and self-organized dynamics

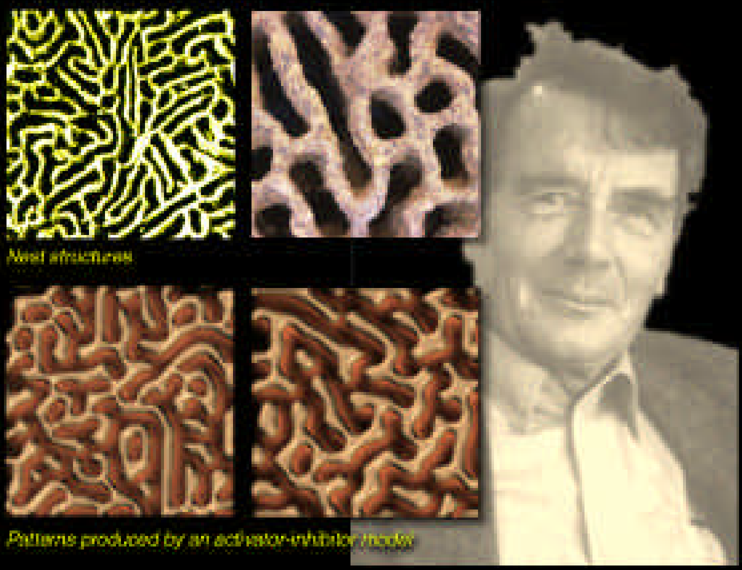
Three important signatures of self-organization

- The emergence of spatio-temporal structures in an initially homogeneous medium through the amplification of fluctuations
- The possible coexistence of several stable states or multistability
- The existence of bifurcationswhen some parameters are varied, a small change in a self-organized system parameter can result in a large change in the overall behaviour of the system


Hans Meinhardt
Pattern formation by local self-enhancement
and long range inhibition
1972
A theory of biological pattern formation.
Kybernetik, 12, 30-39

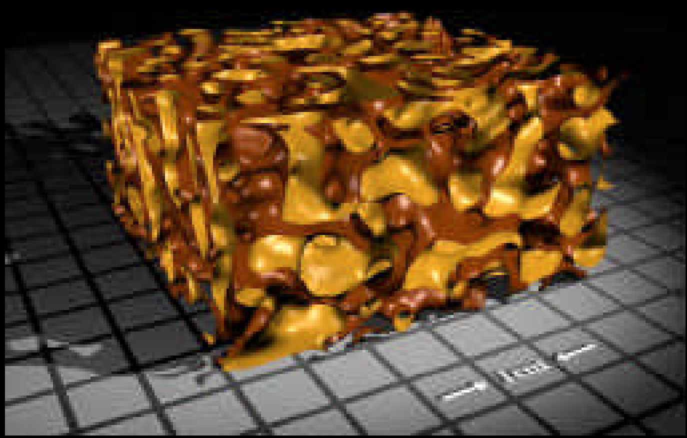

Are these patterns resulting from local activation
and long range inhibition mechanism ?
Fungus growing termites
Lasius fuliginosus
Nasutitermes

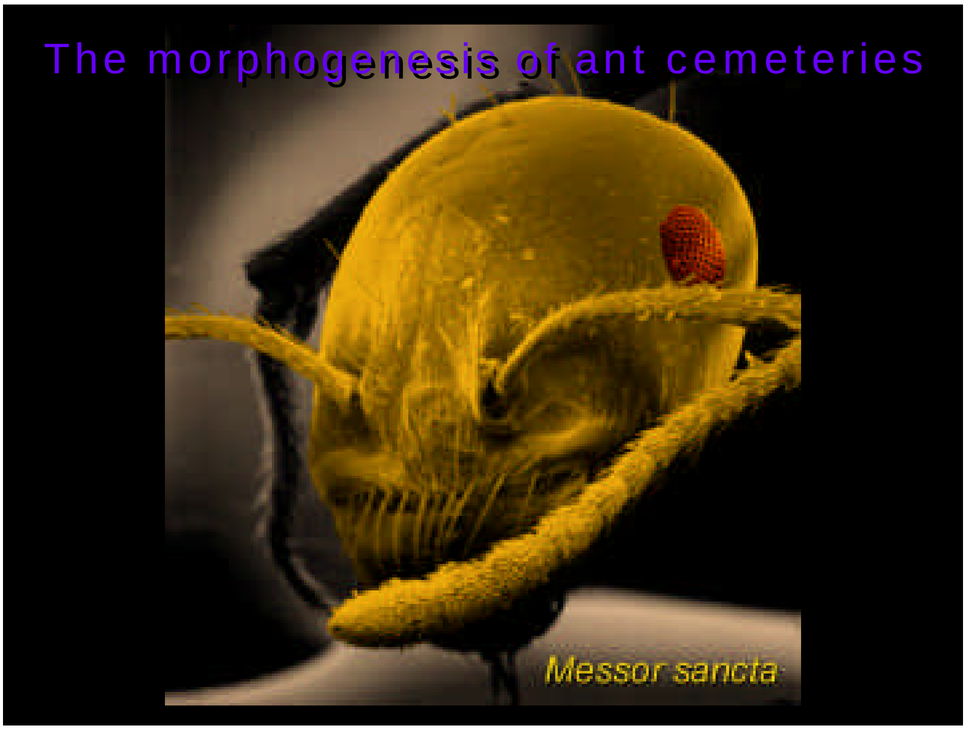
Similar structures

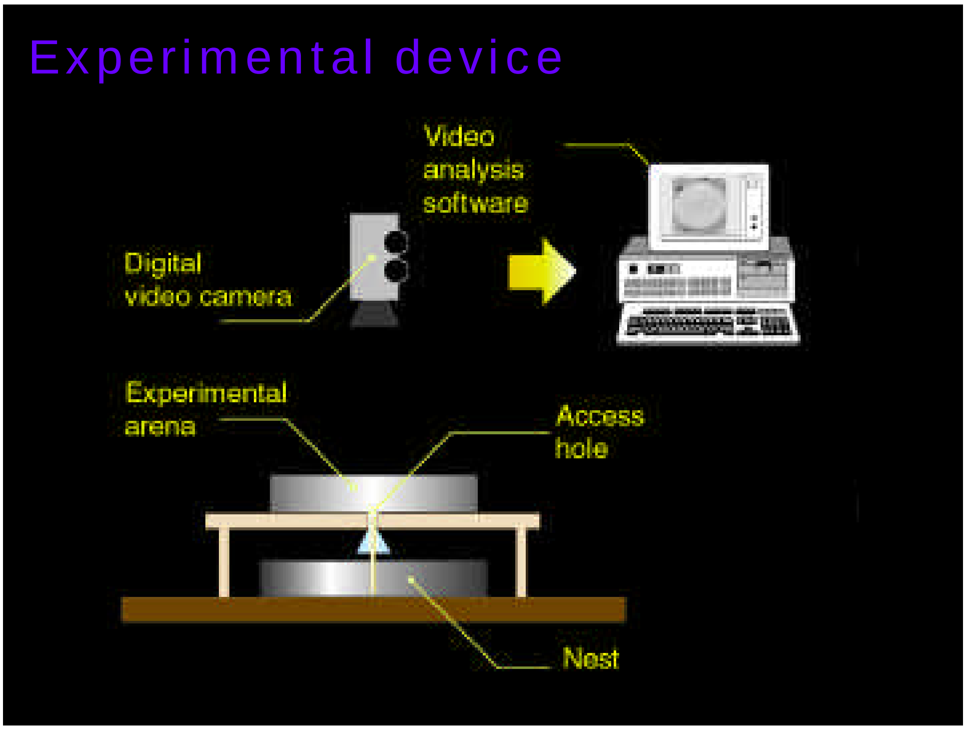


Sponge-like structures

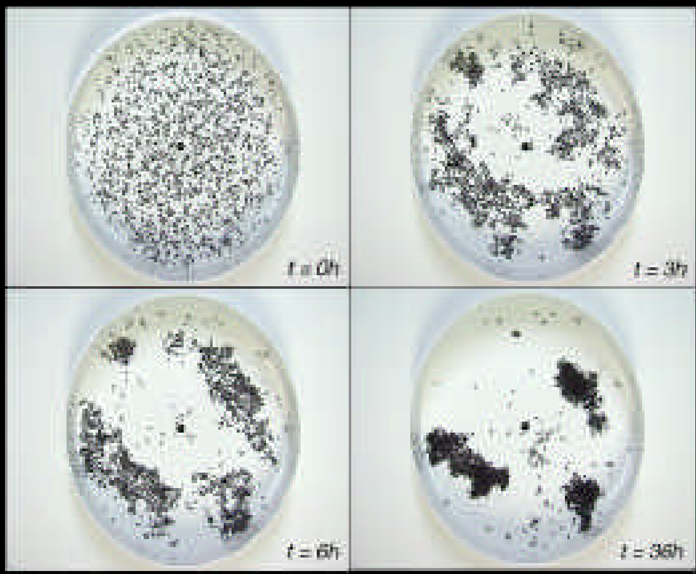
X-ray tomography of a 65mm x 65mm x 33mm section of a termite nest




The morphogenesis of ant cemeteries
Messor sancta


Experimental device
Video
analysis
software
Digital
video camera
Experimental
arena
Access
hole
Nest

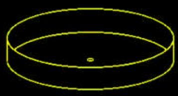
Corpses aggregation on a surface



Dynamics of aggregation on a surface

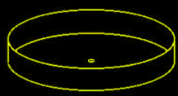
Initial experimental conditions

100 corpses

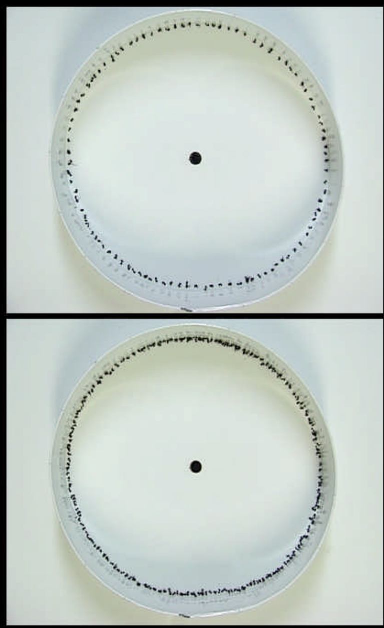


Ø: 25 cm

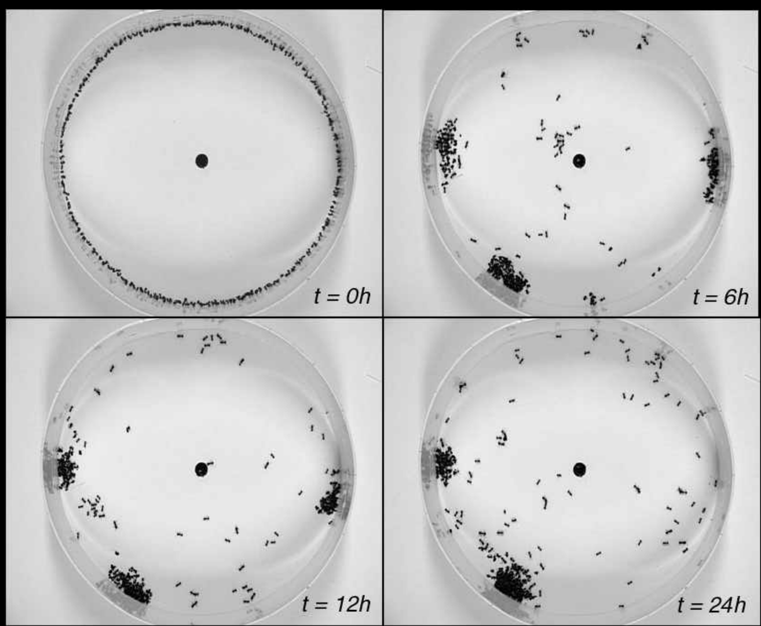
200 corpses



Ø: 25 cm



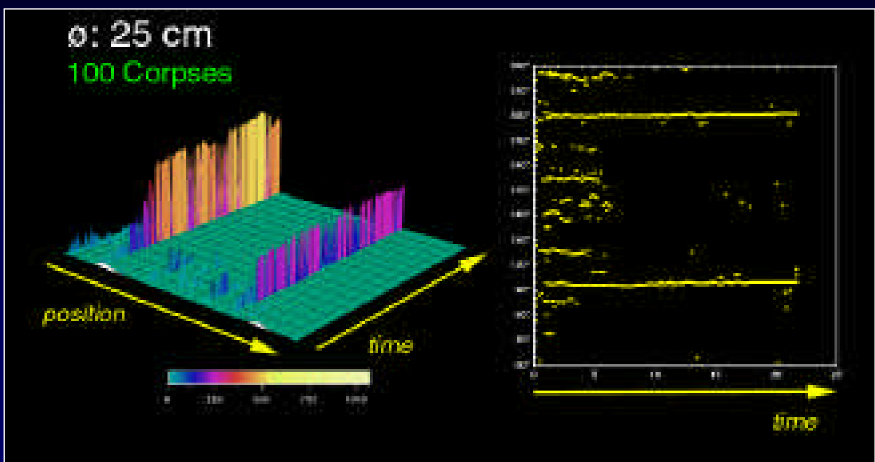
Dynamics of aggregation



Dynamics of aggregation on the edge of the arena

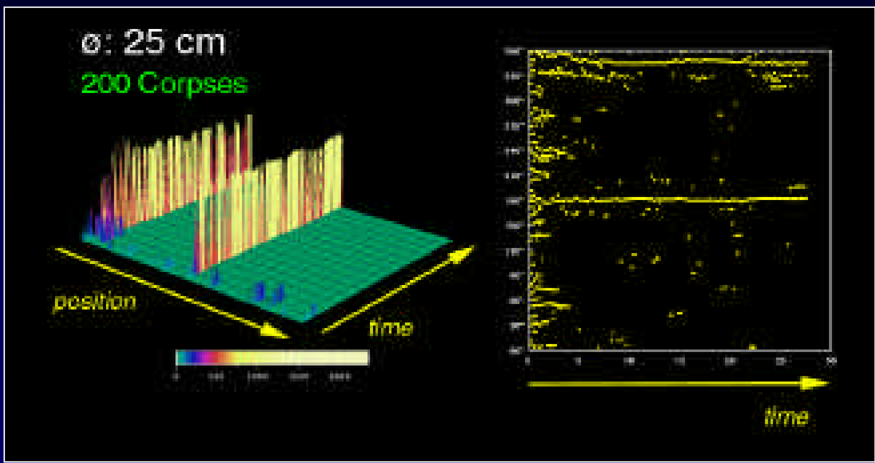
Corpses aggregation in ants

Spatio-temporal dynamics



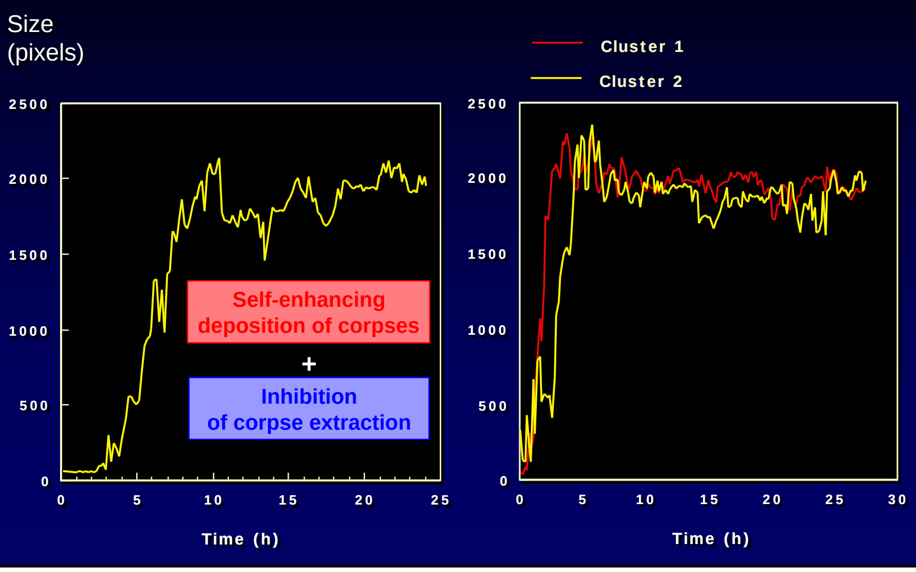
Corpses aggregation in ants

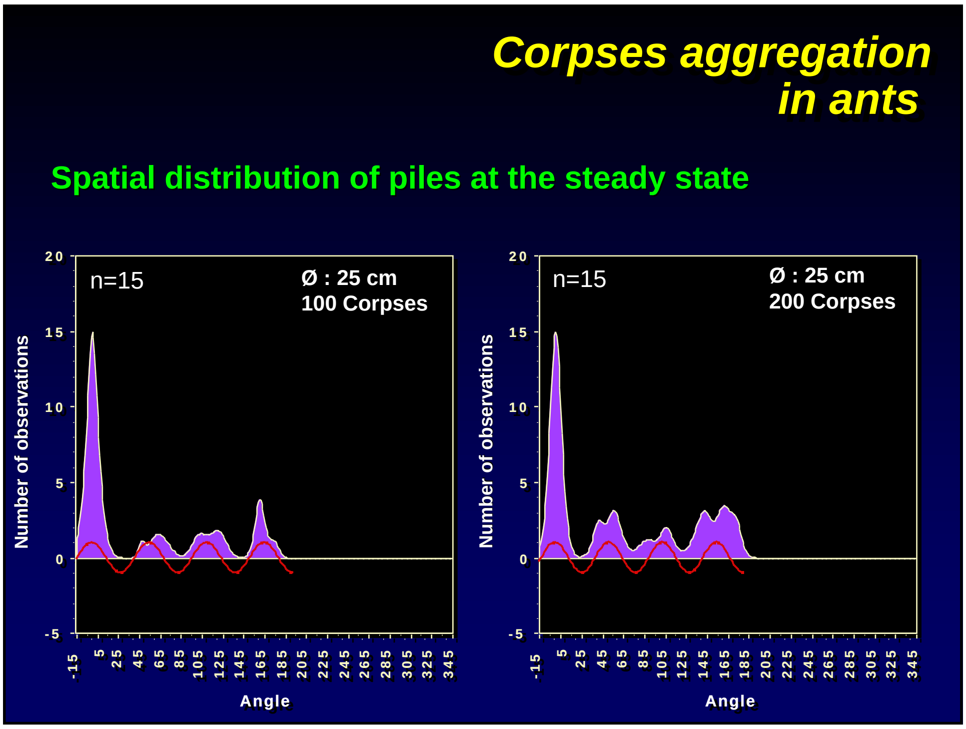
Spatio-temporal dynamics



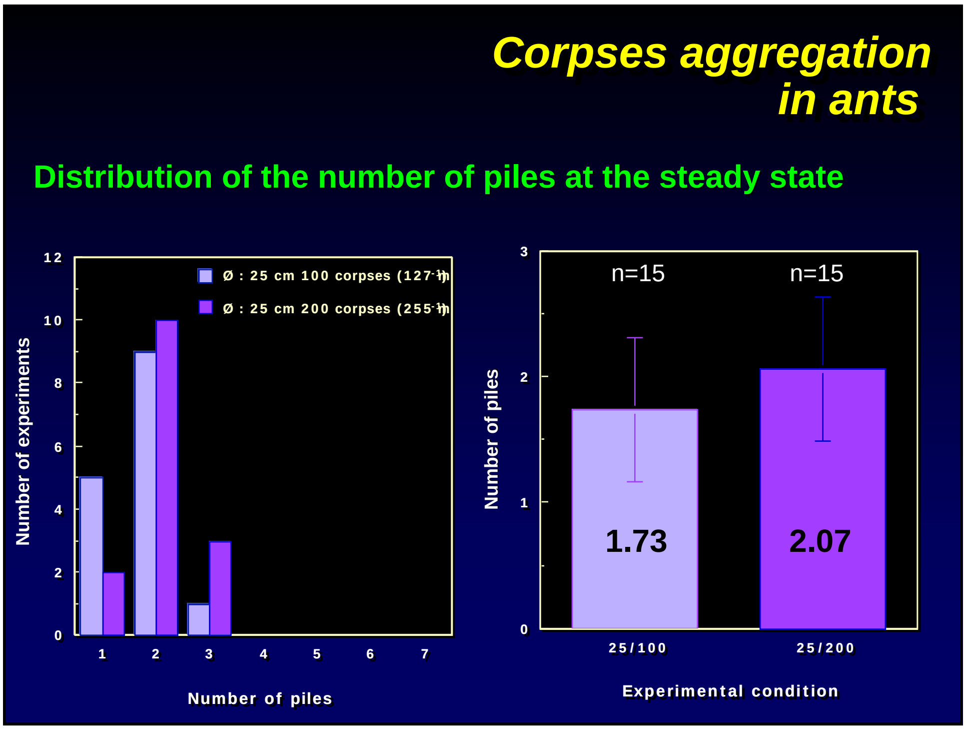
Corpses aggregation in ants

Growth of surviving clusters





Corpses aggregation
in ants
Spatial distribution of piles at the steady state
n=15
Ø : 25 cm
100 Corpses
Number of observations
Angle
n=15
Ø : 25 cm
200 Corpses
Number of observations
Angle



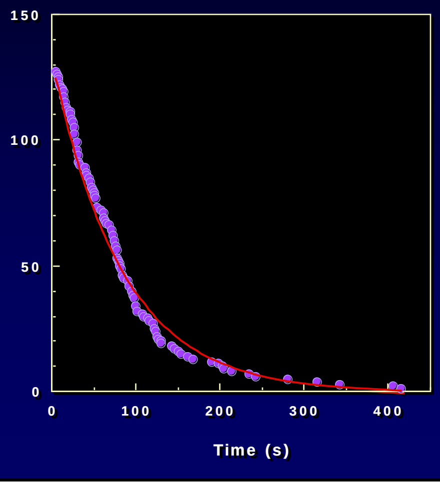
Corpses aggregation
in ants
Distribution of the number of piles at the steady state
Ø : 25 cm 100 corpses (127
Ø : 25 cm 200 corpses (255
Number of experiments
Number of piles
n=15
n=15
1.73
2.07
Number of piles
25/100
25/200
Experimental condition

Underlying microscopic rules of the ants’ behaviour

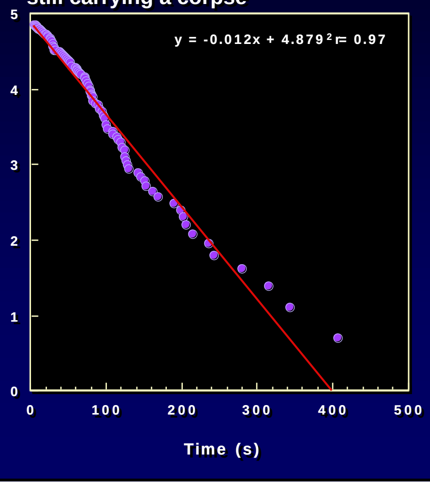
Aggregation mechanisms at the individual level

Spontaneous dropping probability

$\delta = 0.012 \text{ sec}^{-1}$



Natural log of the number of ants still carrying a corpse



Aggregation mechanisms at the individual level

Probability of picking up a corpse as a function of the size of the pile

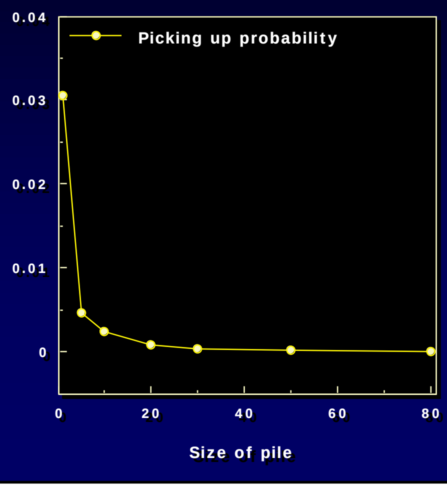
$$P_{picking} = \frac{P}{L+C_i}$$

P : number of non-carrying ants having picked-up a corpse on the pile

L : total number of non-carrying ants that walked over the pile

C_i : total number of corpses in the pile i

The duration of the picking up behaviour is relatively long (≈ 15 s)



Aggregation mechanisms at the individual level

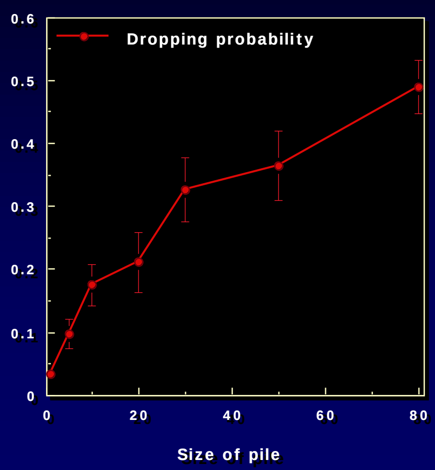
Probability of dropping a corpse as a function of the size of the pile

$$P_{dropping} = \frac{L}{P}$$

L : number of corpse-carrying ants having dropped the corpse on the pile

P : total number of corpse-carrying ants that walked over the pile

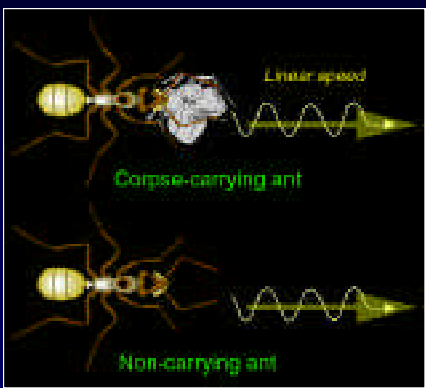
The duration of the dropping behaviour is relatively long (≈ 15 s)

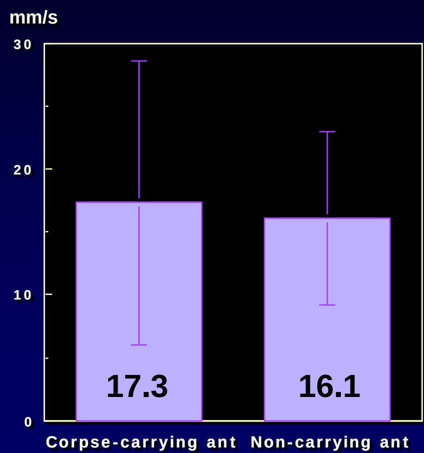


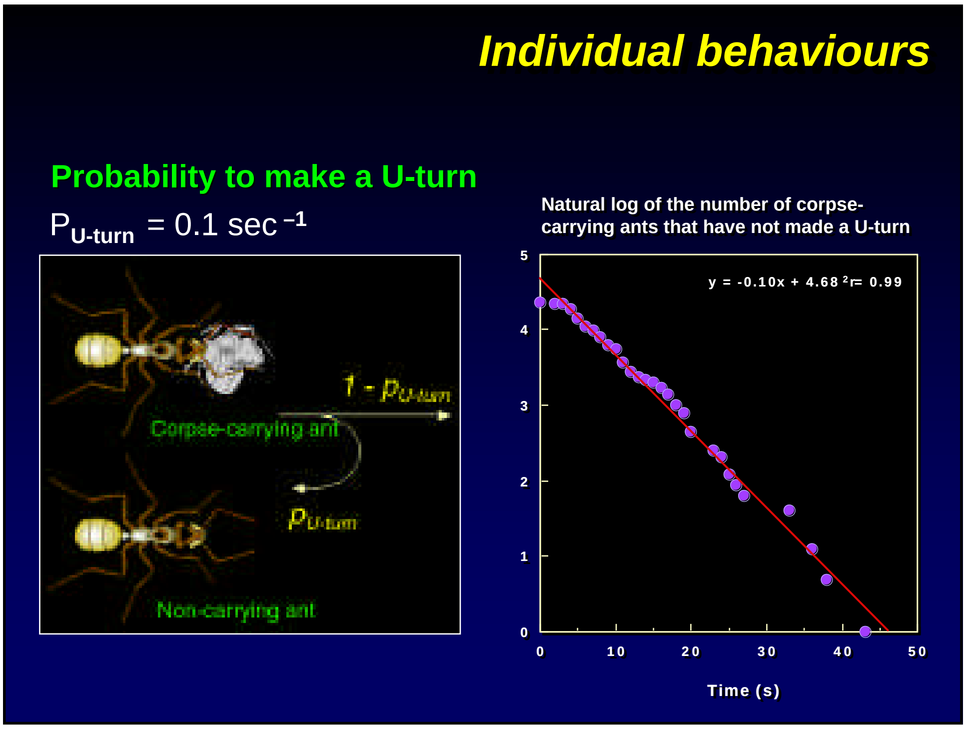
Ants’ displacement

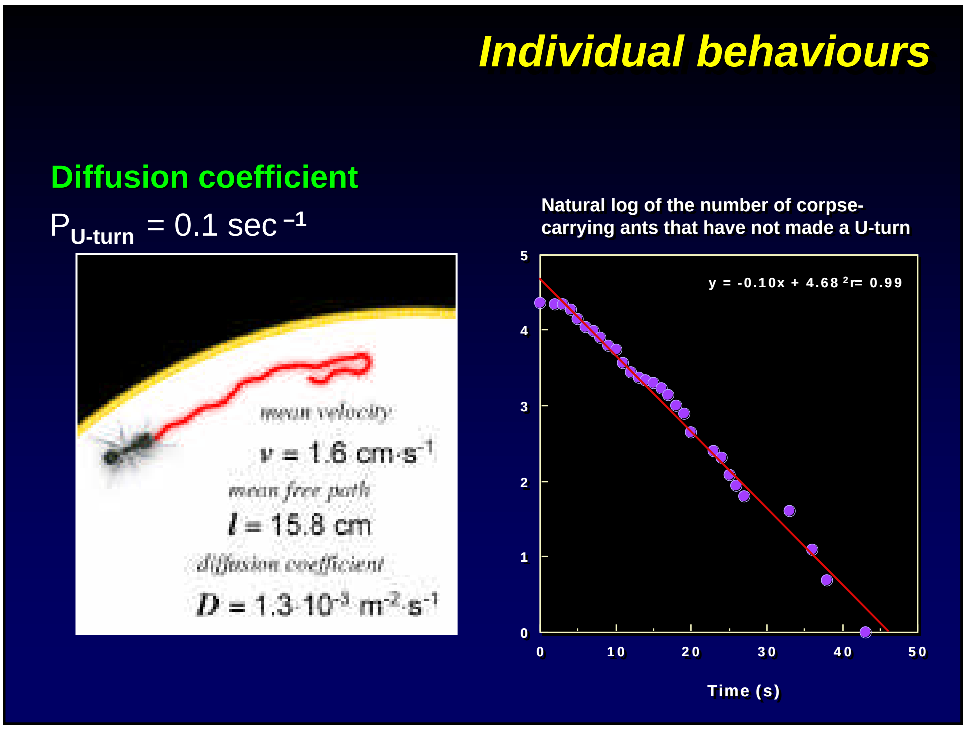
Individual behaviours

Linear speed



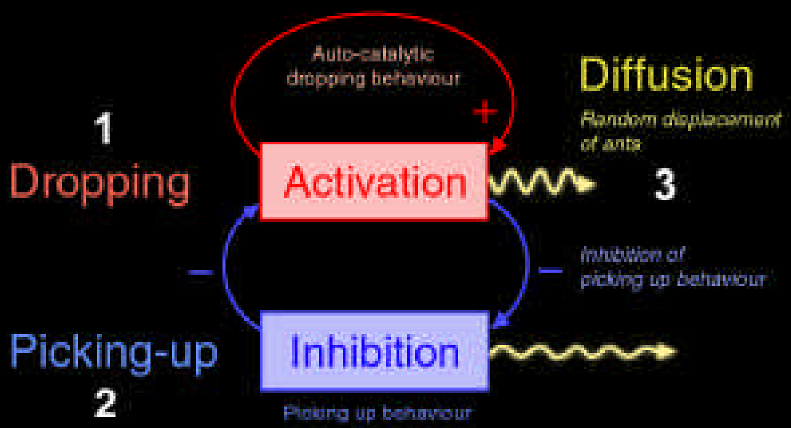



Individual behaviours
Probability to make a U-turn
P U-turn = 0.1 sec -1
1 - p U-turn
Corpse-carrying ant
p U-turn
Non-carrying ant
Natural log of the number of corpse-carrying ants that have not made a U-turn
y = -0.10x + 4.68 r² = 0.99
0
1
2
3
4
5
0
10
20
30
40
50
Time (s)


Individual behaviours
Diffusion coefficient
P U-turn = 0.1 sec -1
mean velocity
v = 1.6 cm·s-1
mean free path
l = 15.8 cm
diffusion coefficient
D = 1.3·10-3 m2·s-1
Natural log of the number of corpse-carrying ants that have not made a U-turn
y = -0.10x + 4.68 r² = 0.99
0
1
2
3
4
5
0
10
20
30
40
50
Time (s)

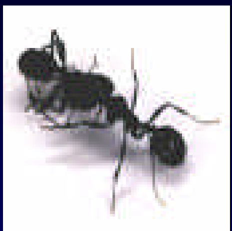
Modeling the dynamics of corpses aggregation

Mechanisms taking place in corpses aggregation



A model of the dynamics of spatial aggregation

Model description



- 3 variables

  c : density of corpses on the arena
  a : density of corpse-carrying ants
  ρ : density of non-carrying ants

- Equations (continuous model)

  δc/dt = **dropping term** – **picking up term**

  δa/dt = **picking up term** – **dropping term** ± **displacement term**

  $\int_{length} (c + a)\ dl = \text{constant}$

  ρ is assumed to remain uniform and constant over time in the model

Continuous model of corpses aggregation in ants

Density of corpses (c)

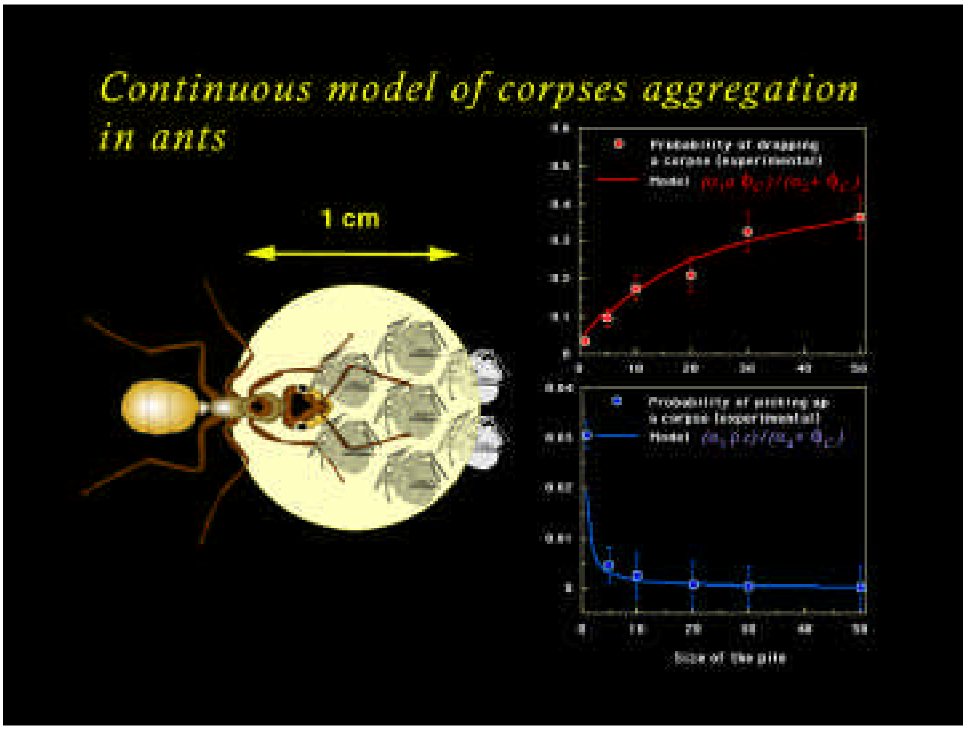
$$\partial c / \partial t = \nu \left[k_d\, a + (\alpha_1 a\, \phi_C)/(\alpha_2 + \phi_C) - (\alpha_3 \rho\, c)/(\alpha_4 + \phi_C) \right]$$

Density of corpse-carrying ants (a)

$$\partial a / \partial t = \nu \left[- k_d\, a - (\alpha_1 a\, \phi_C)/(\alpha_2 + \phi_C) + (\alpha_3 \rho\, c)/(\alpha_4 + \phi_C) \right] + D\, \partial^2 a / \partial x^2$$

ϕ_C : non-local term introducing a short-range interaction between workers and corpses

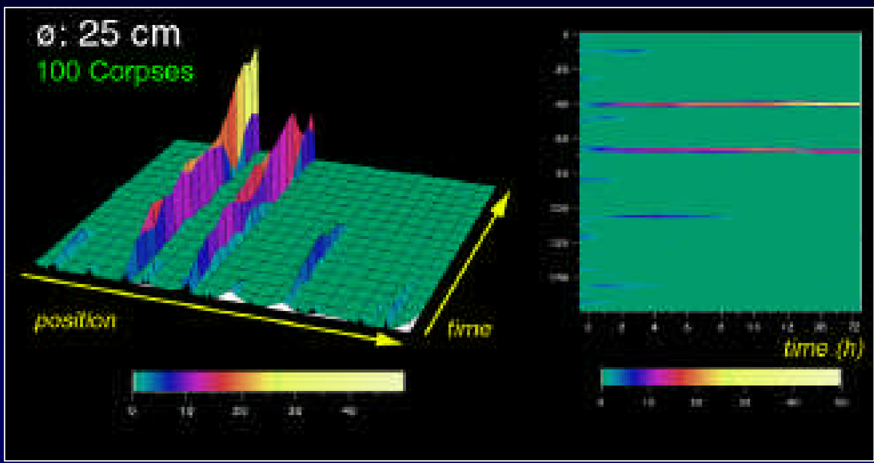
$$\phi_C = \frac{1}{2\Delta} \int_{x-\Delta}^{x+\Delta} c(z)\, dz$$



Results
Monte Carlo simulation

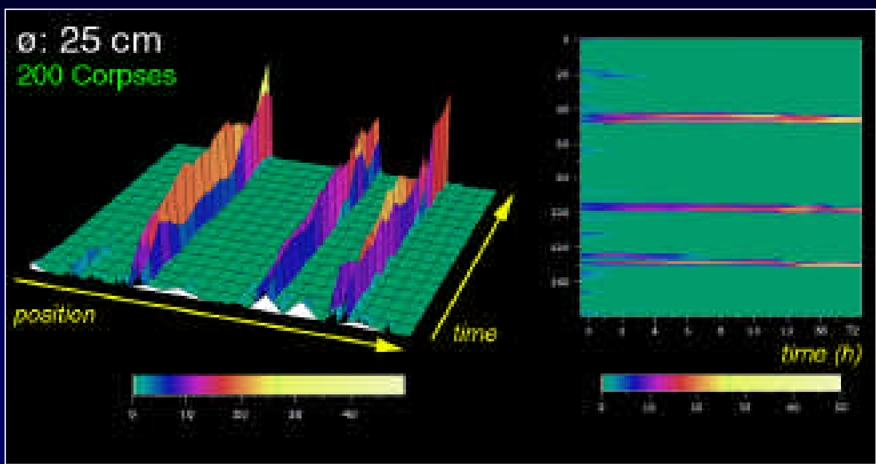
Simulation of corpses aggregation

Spatio-temporal dynamics



Simulation of corpses aggregation

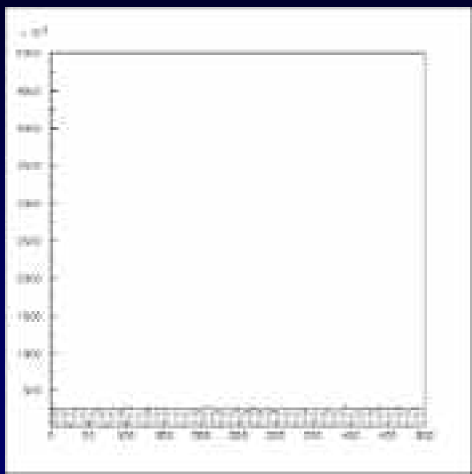
Spatio-temporal dynamics



Simulation of corpses aggregation

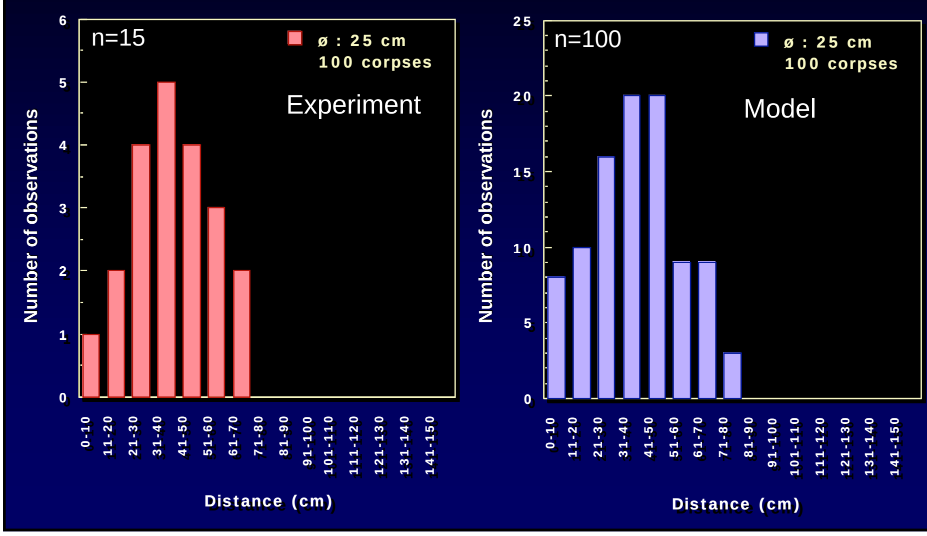
Spatio-temporal dynamics

Ø:25 cm 200 corpses



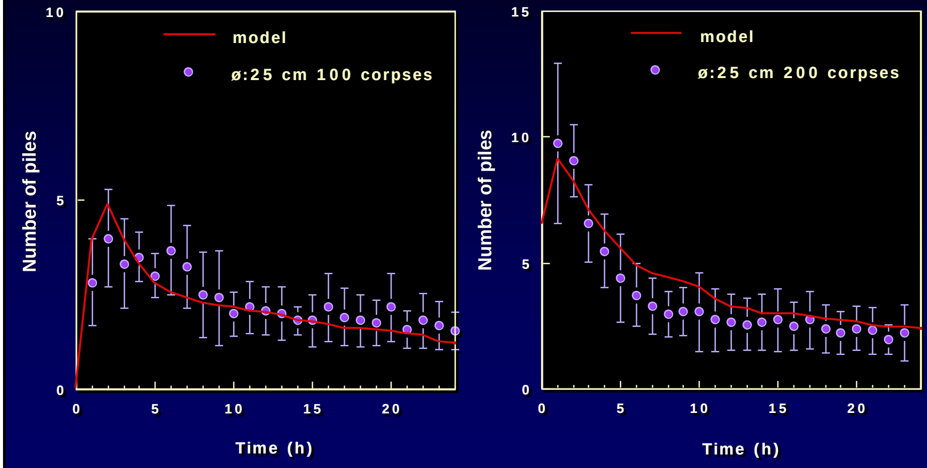
Comparison of the model's predictions with experimental results

Distribution of inter-pile distances

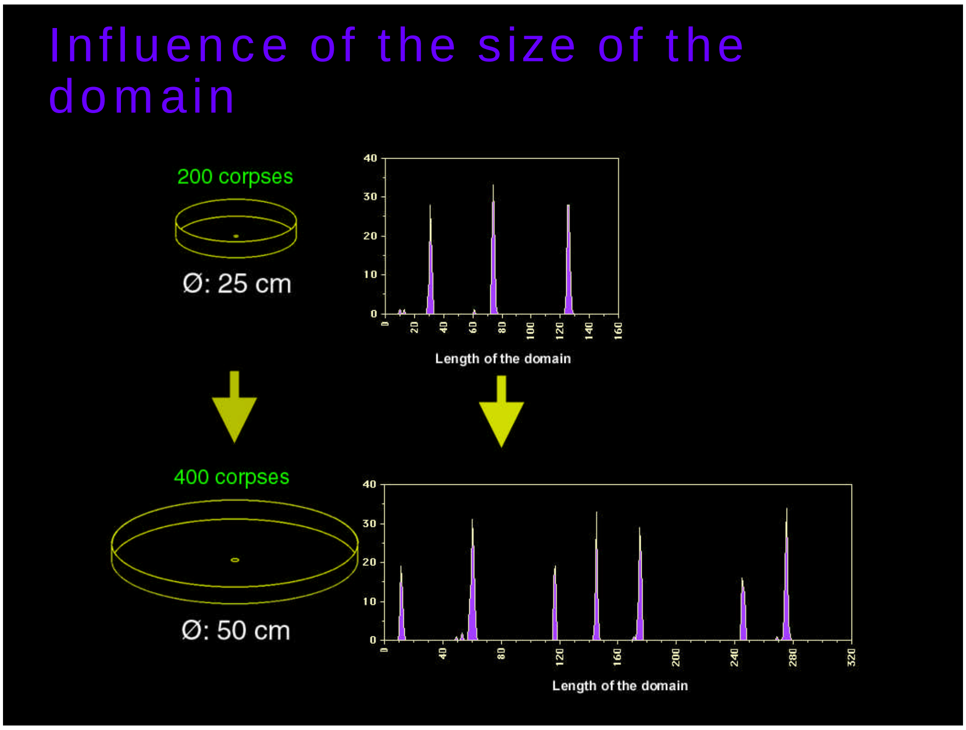


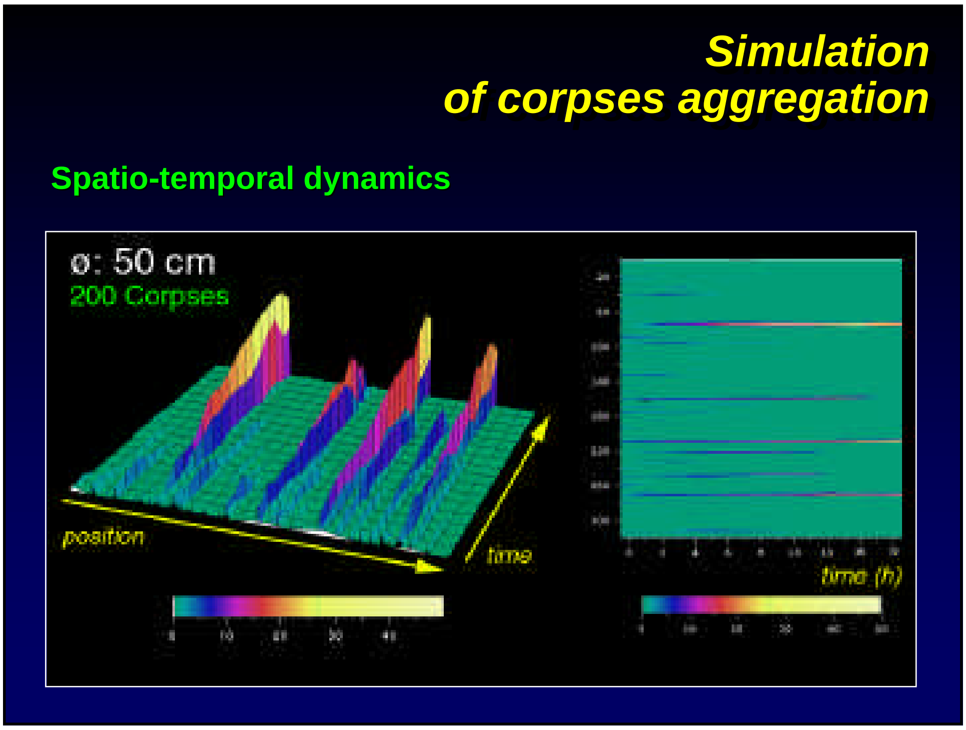
Comparison of the model's predictions with experimental results

Evolution of the mean number of piles



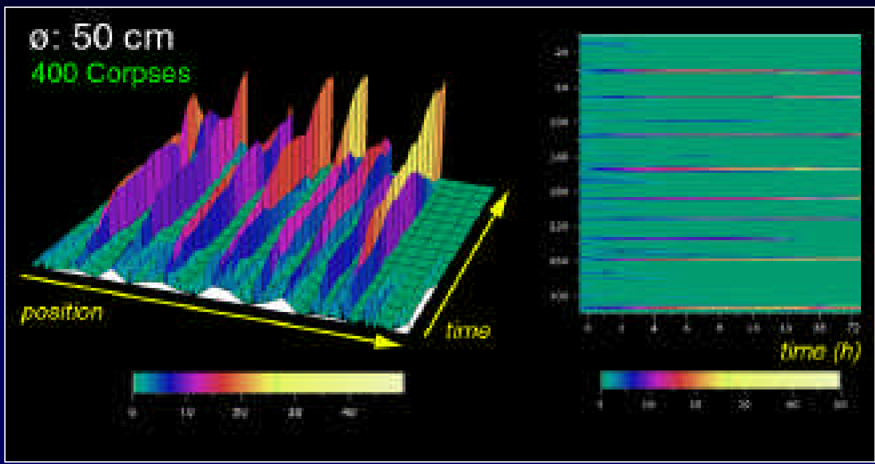
Model predictions


Influence of the size of the domain
200 corpses
Ø: 25 cm
Length of the domain
400 corpses
Ø: 50 cm
Length of the domain


Simulation
of corpses aggregation
Spatio-temporal dynamics
ø: 50 cm
200 Corpses
position
time
time (h)

Simulation of corpses aggregation

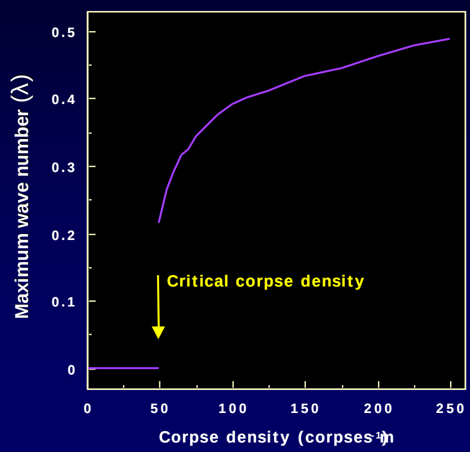
Spatio-temporal dynamics



Stability analysis

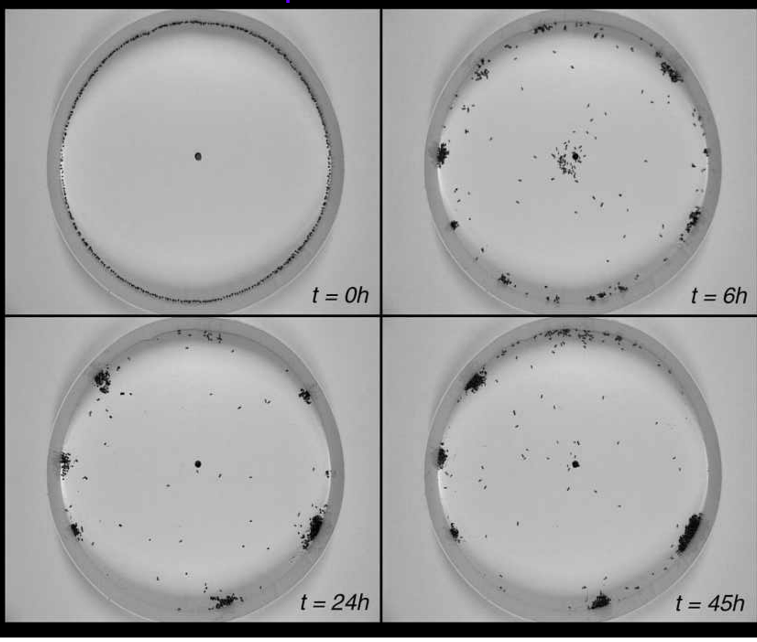
Solution of the characteristic equation

A critical density of corpses exists below which no aggregation occurs



Testing model predictions

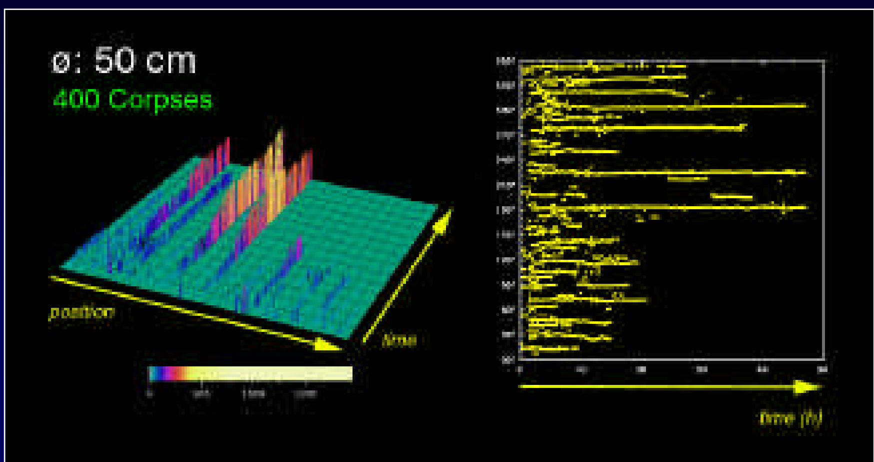
Aggregation dynamics in a 50 cm diameter arena and 400 corpses

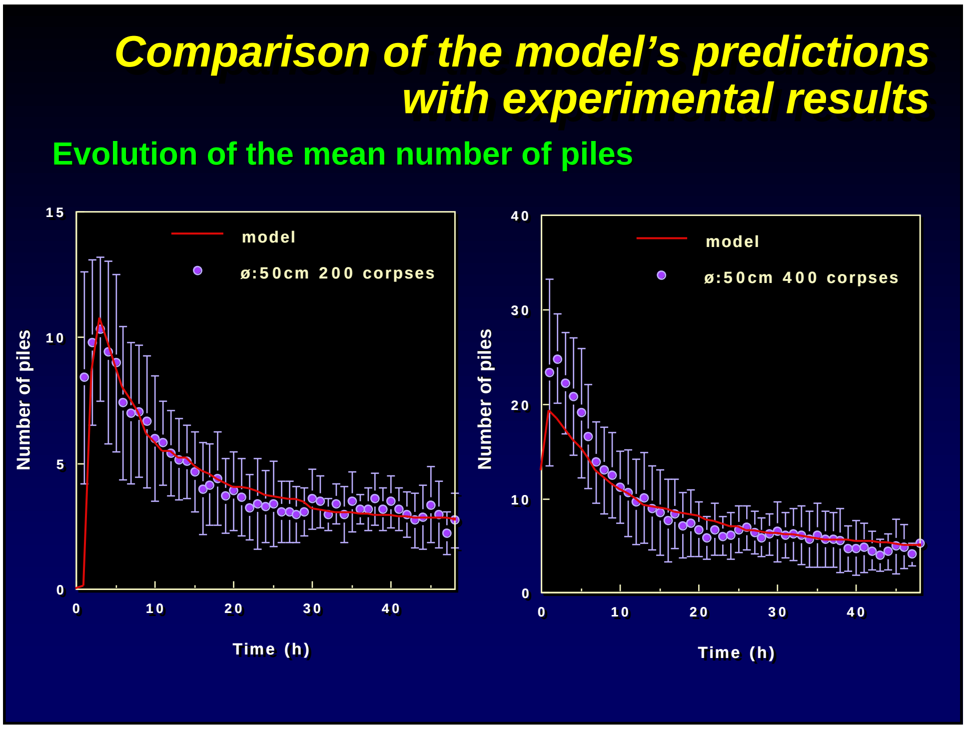


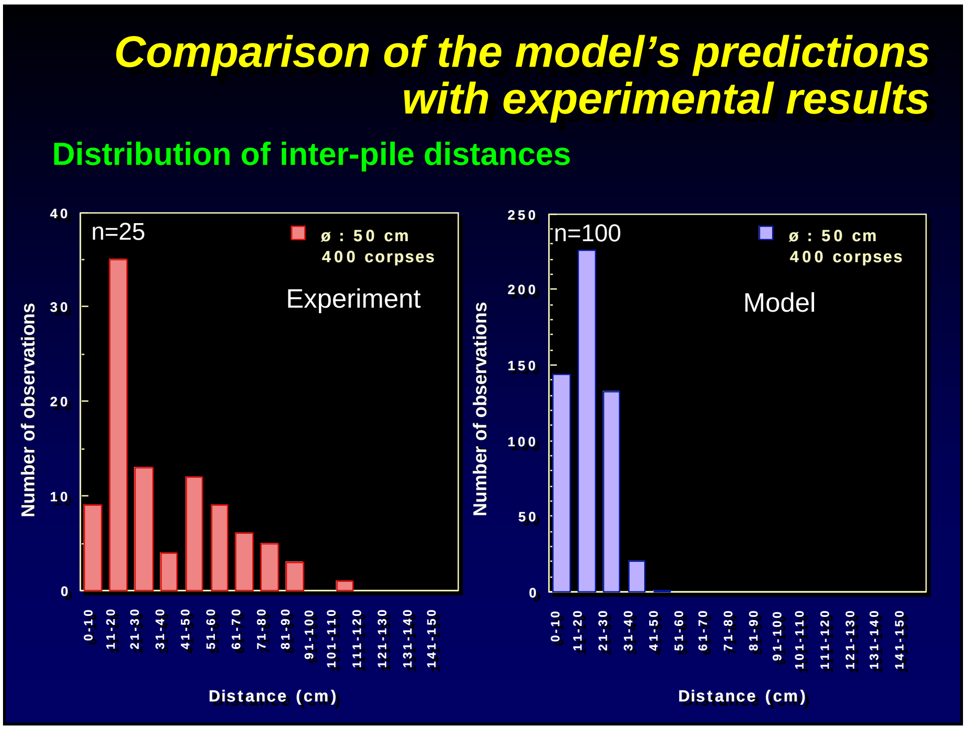
Recording of the aggregation dynamics with a 50 cm diameter arena and 400 corpses

Corpses aggregation in ants

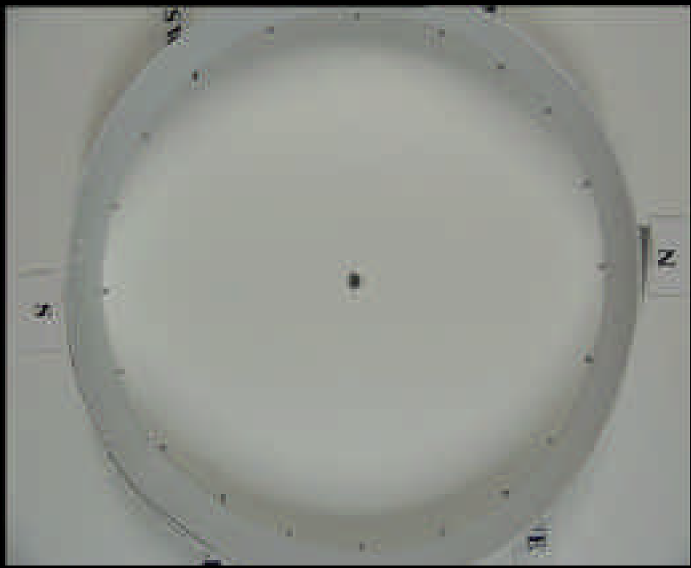
Spatio-temporal dynamics




Comparison of the model's predictions
with experimental results
Evolution of the mean number of piles
model
ø:50cm 200 corpses
Number of piles
Time (h)
model
ø:50cm 400 corpses
Number of piles
Time (h)


Comparison of the model's predictions
with experimental results
Distribution of inter-pile distances
n=25
ø : 50 cm
400 corpses
Experiment
Number of observations
Distance (cm)
n=100
ø : 50 cm
400 corpses
Model
Number of observations
Distance (cm)

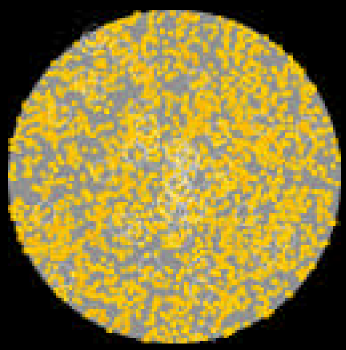
Aggregation dynamics below the critical density (50 cm diameter arena and 20 corpses)



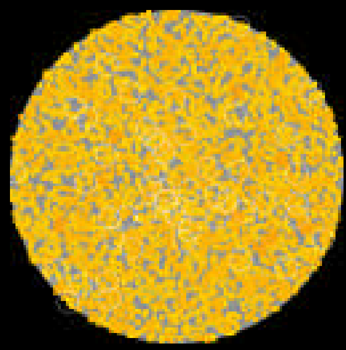
2D Monte Carlo simulation

2D Monte Carlo simulation

Spatio-temporal dynamics in a circular arena



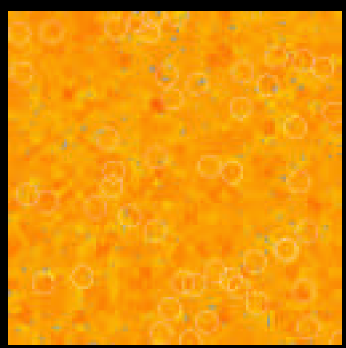
Ø:30 cm 2000 corpses (3 days)



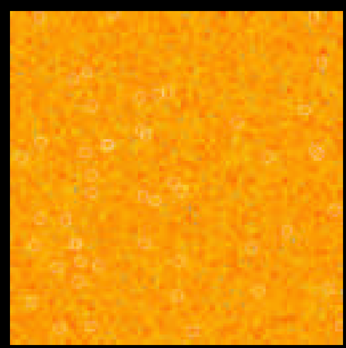
Ø:30 cm 4000 corpses (6 days)

2D Monte Carlo simulation

Spatio-temporal dynamics in a square arena

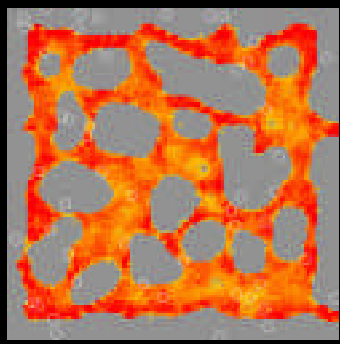


30X30 cm 16000 corpses (40 days)



60X60 cm 64000 corpses (103 days)

2D Monte Carlo simulation



Cubitermes

Collective nest building could result from similar rules to those used by ants to aggregate their corpses

The morphogenesis of ant cemeteries by Turing-type instability

- The formation of cemeteries in ants is an example of Local-activation Long-range inhibition morphogenesis
- All the behavioural parameters of the model were quantified in dedicated experiments
- When loaded with the experimental parameter values, the model not only leads to the formation of patterns that reproduce the properties of cemetery formation, but also predicts how the pattern is affected by experimental characteristics such as corpse density and arena size

Stigmergy and self-organized dynamics

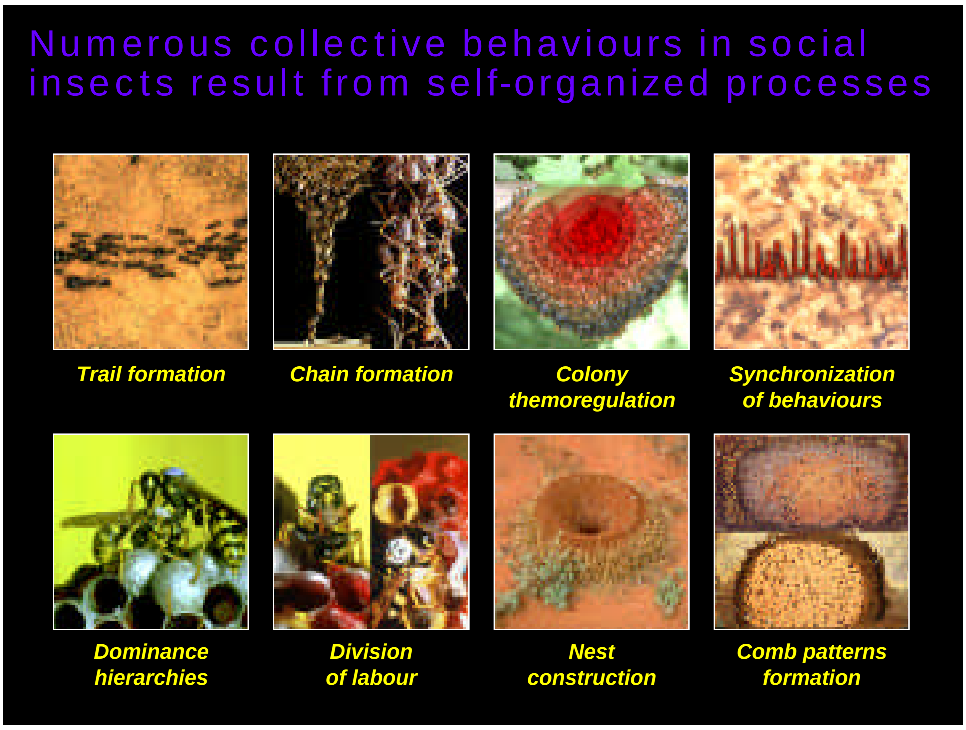
- Several experimental evidences show that numerous other social phenomena (building behaviour, brood and seeds sorting in ant colonies) should result from similar processes (local amplification and spatial competition)

Morphogenesis of galleries networks in the ant Messor sancta

Morphogenesis of a bifurcation

Conclusions

- Competition between local amplification and diffusion processes can generate regularly spatial structures and might be a general morphogenetic principle at work in social insects
- Sophisticated structures and complex architectural patterns might be explained by the combination of a small number of simple mechanisms and the interplay of simple individual behaviours with varying external as well as internal conditions
- Self-organized processes are a major component of a wide range of collective phenomena in social insects


Numerous collective behaviours in social insects result from self-organized processes
Trail formation
Chain formation
Colony themoregulation
Synchronization of behaviours
Dominance hierarchies
Division of labour
Nest construction
Comb patterns formation