Biological principles of swarm intelligence

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Biological principles of swarm intelligence

A single ant or bee isn't smart
… but their colonies are !!

Biological principles of swarm intelligence

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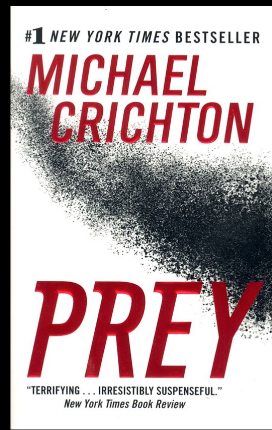
… but their colonies are !!

The study of swarm intelligence is providing insights that can help humans manage complex systems

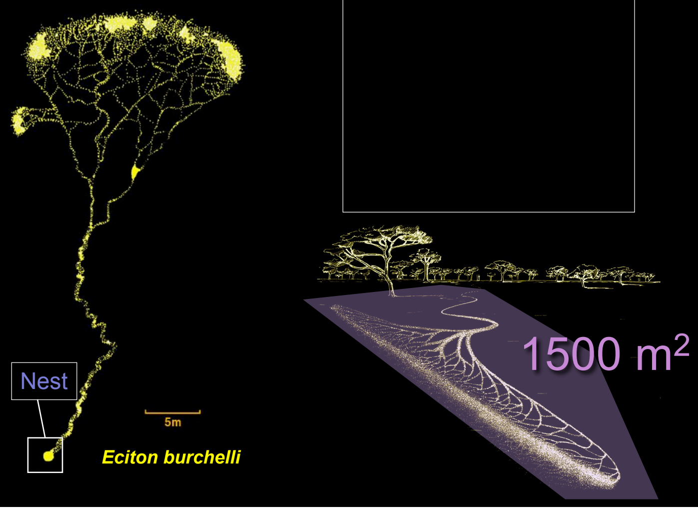
The "spirit of the hive" revived

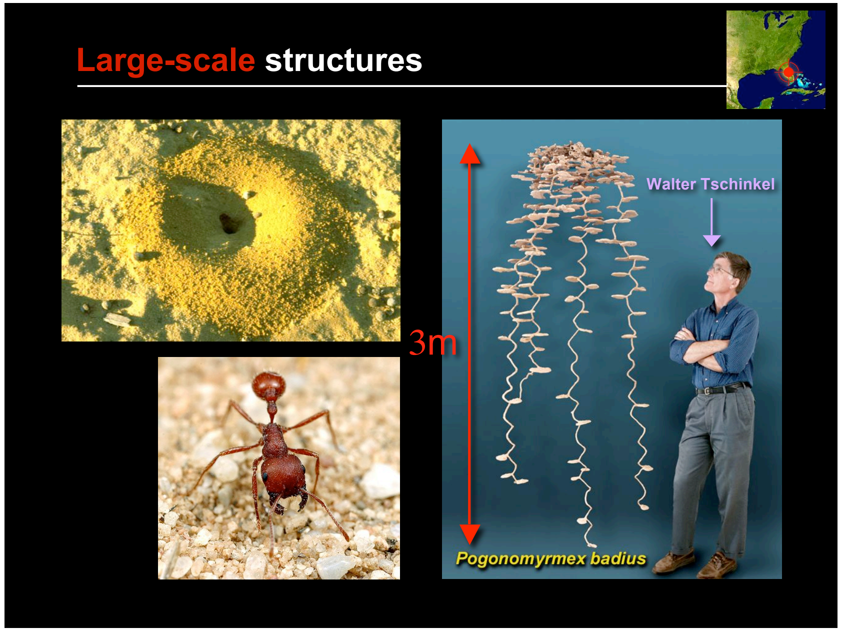


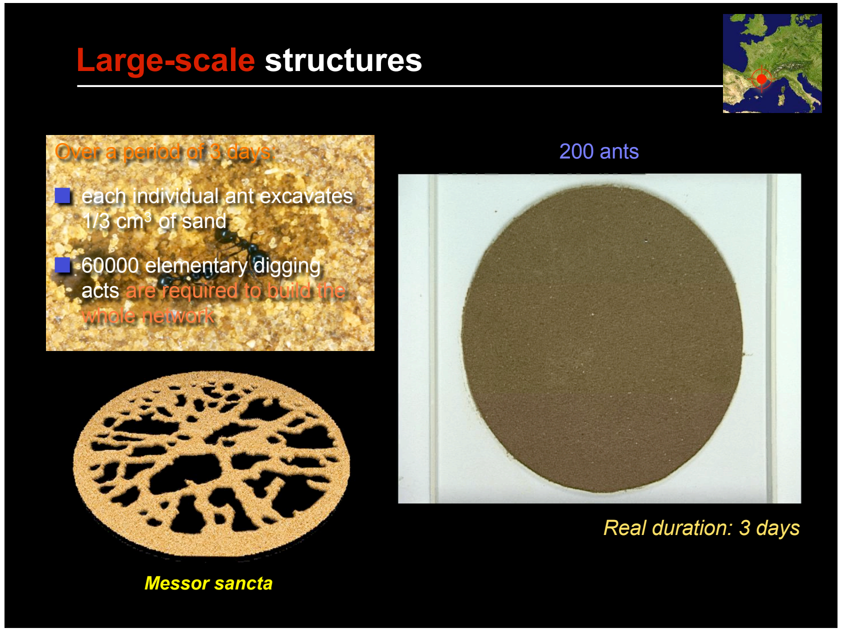
The “spirit of the hive” revived

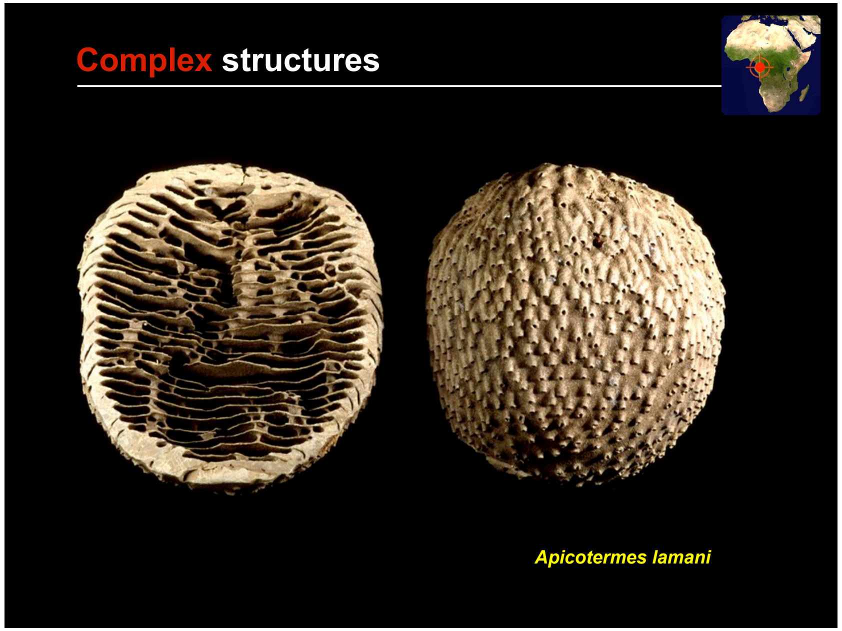
The Swarm, (1978)
Director: Irwin Allen, Warner Bros Pictures

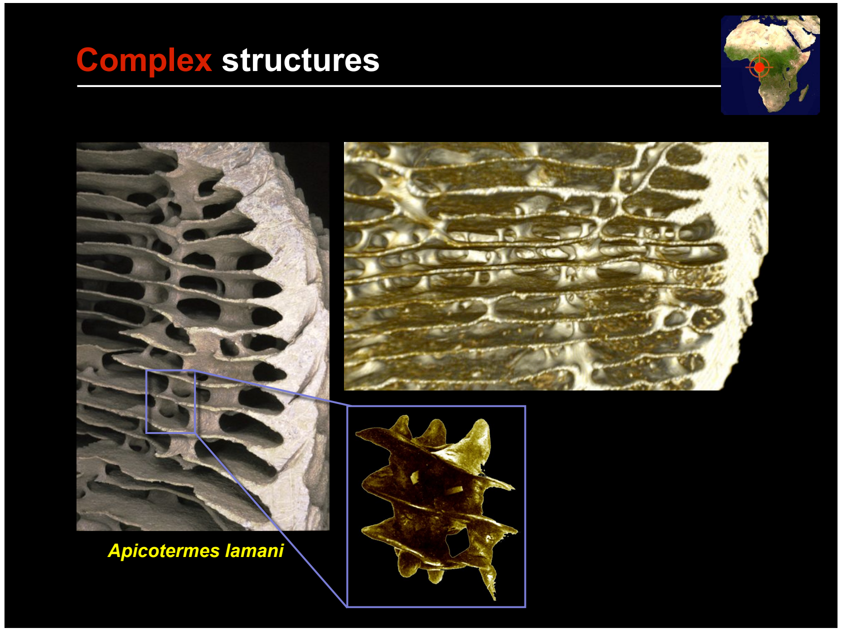
Large-scale networks




Large-scale structures
Walter Tschinkel
3m
Pogonomyrmex badius


Large-scale structures
Over a period of 3 days:
each individual ant excavates 1/3 cm³ of sand
60000 elementary digging acts are required to build the whole network
Messor sancta
200 ants
Real duration: 3 days


Complex structures
Apicotermes lamani


Complex structures
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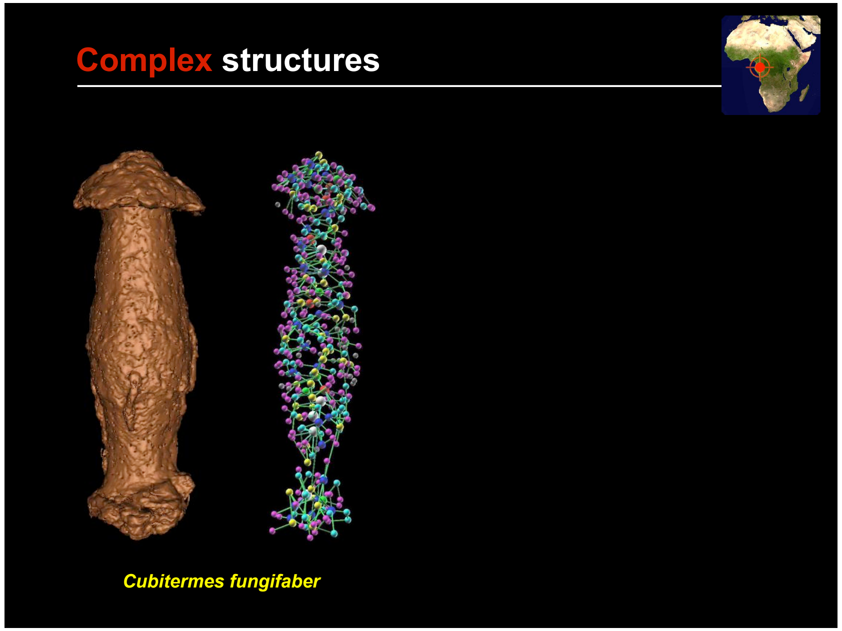
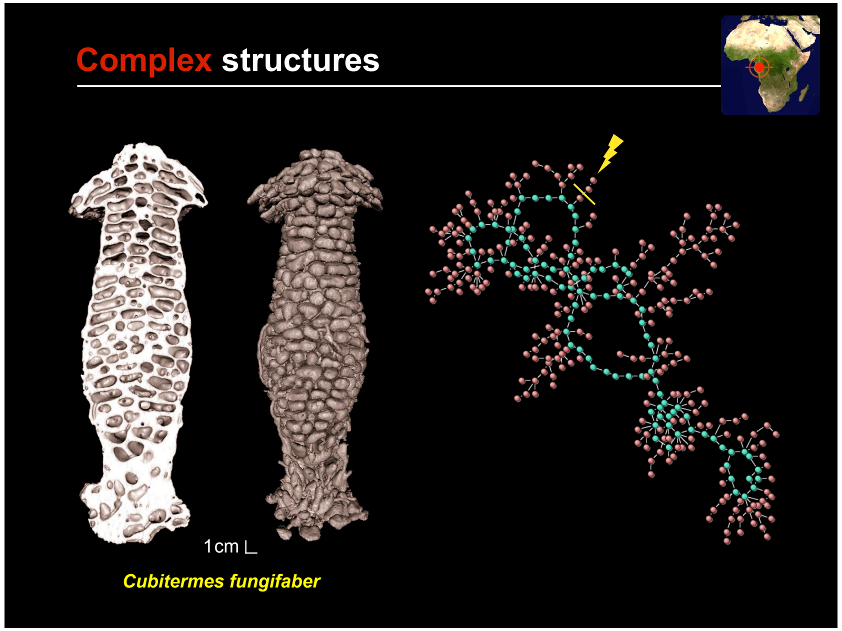
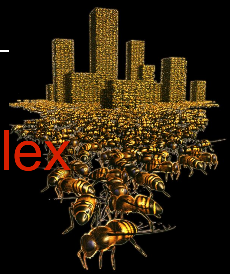
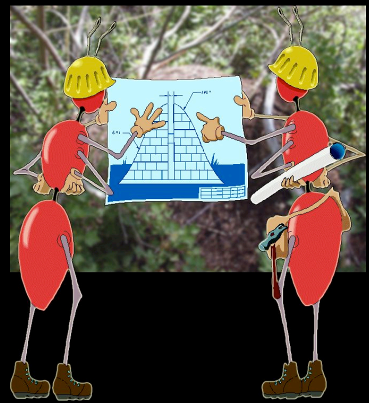

Complex structures
Cubitermes fungifaber


Complex structures
1cm
Cubitermes fungifaber

The underlying mechanisms of complex collective behaviors

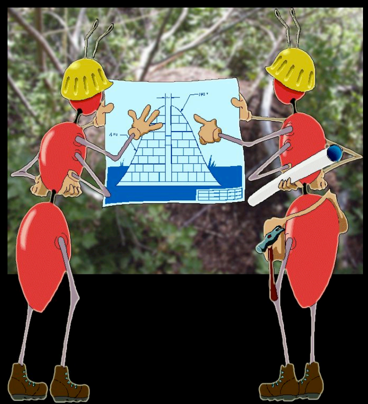


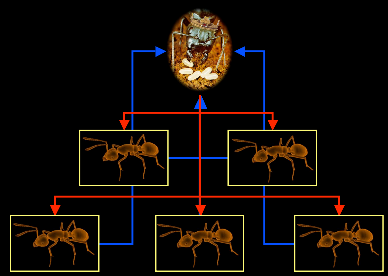
The anthropomorphic hypothesis



- The complexity of behaviors and patterns observed at the colony level should be a direct consequence of the individuals ability:
  - to centralize information about the environmental conditions
  - to build an internal representation of these conditions and then …
  - to choose the appropriate actions to perform

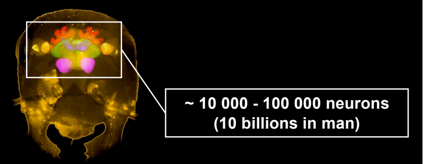
A centralized organization





- Information coming from the colony was supposed to be gathered and monitored by the queen which then controls and supervises workers activities

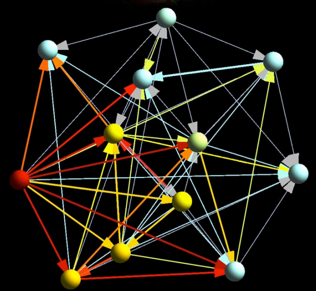
The society has no supervisor



- Individual insects do not have a mental blueprint of the architectures they build or a global representation of the state of the colony
- Their cognitive system is not enough powerful for a single individual to assess a global situation, centralize all the information coming from its colony and then control the tasks to be done by the other workers

Social insects colonies are distributed information processing systems

Social interaction network in Polistes wasps



- **Emergent properties**

  Complex collective behaviors emerge from interactions among individuals

- **Local information**

  The rules specifying the interactions among insects are executed on the basis of purely local information, without any knowledge of the global pattern

- **A limited set of instructions**

  Each insect is following a small set of simple behavioral rules (≈ 20 elementary behaviors in ants)

Pierre-Paul Grassé (1895-1985)

The stigmergy

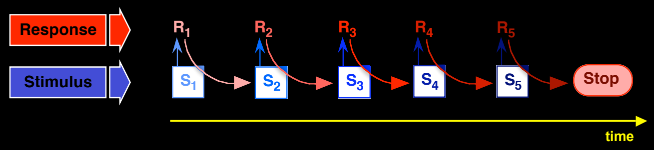
1959

La reconstruction du nid et les coordinations inter-individuelles chez *Bellicositermes natalensis* et *Cubitermes sp.* La théorie de la stigmergie : essai d'interprétation du comportement des termites constructeurs.
Insectes Sociaux, **6**, 41-81

"An insect does not control his own work. But its ongoing activity is guided by the by-product of its work"

Stigmergy: invisible writing

- Stigmergy occurs when insect's actions are determined or influenced by the consequences of another insect's previous action
- This is a form of indirect communication that makes possible the coordination and regulation of insects activities



- This process leads to an (almost) perfect coordination of the collective work and gives us the impression that a colony as a whole is following a pre-defined plan

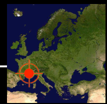
Nest building in social wasps

A stigmergic behavior

- Wasp nests are built with wood pulp and plant fibers
- Colored blotting paper used as building material makes it possible the visualization of successive building steps
- Individual construction behavior can be studied in great details such as the wasps decisions to build a new cell in particular locations on the comb

Nest construction
in *Polistinae* wasps

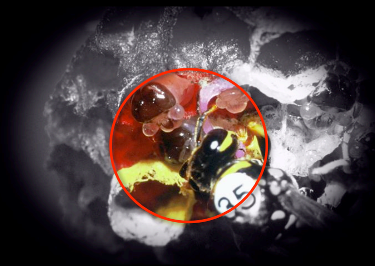
Nest building in social wasps

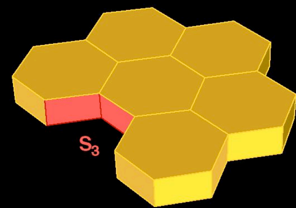


The first construction steps in *Polistes dominulus*

The control of nest building in wasps

Potential building sites on a comb

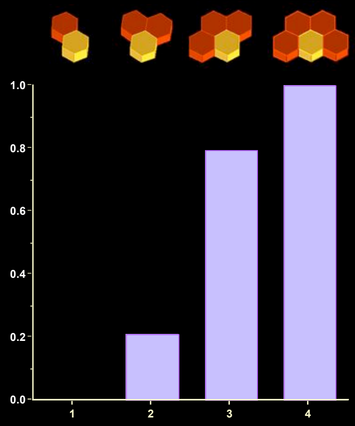




- The nest structure controls the organization of building activities
- To decide where to build a new cell, wasps make use of the information provided by the local arrangement of cells on the comb

Construction rules in Polistes wasps

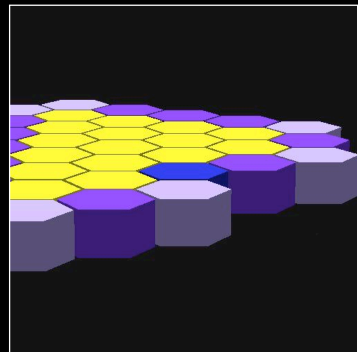
Probability to build a new cell on the comb



- New cells are not added randomly to the existing structure
- Wasps have a greater probability to add new cells to a corner area (3 or 4 adjacent walls) than to initiate a new row by adding a cell on the side of an existing row (2 adjacent walls)

Modeling nest building

Behavior of the virtual wasps

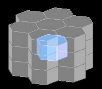


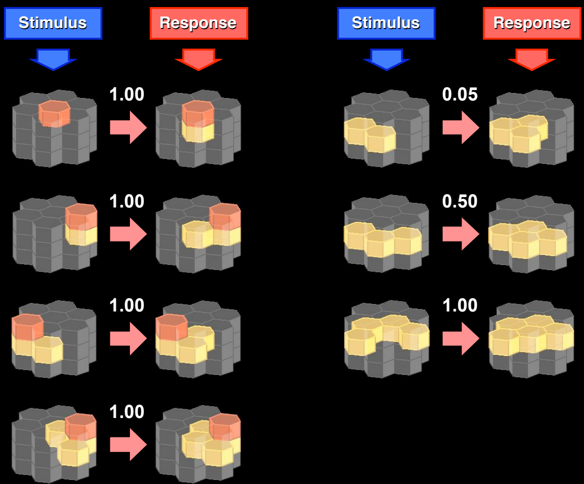
- Wasps are modeled by asynchronous automata with a stimulus-response behavior
- Virtual wasps move randomly in a 3-D discrete hexagonal lattice
- Virtual wasps only have a local perception of their environment (the first 26 neighboring cells close the cell occupied by the wasp)
- … and do not have any representation of the global architecture they build

(Theraulaz, G. & Bonabeau, E., *Science*, 1995)

Modeling nest building

Local construction rules followed by the virtual wasps



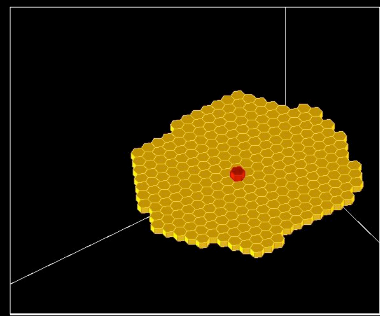


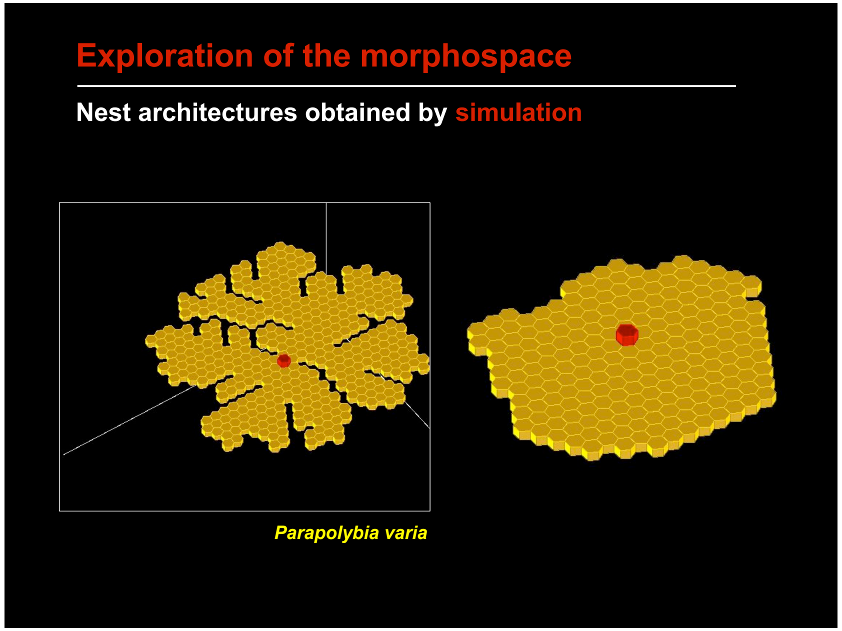
- Some configurations of cells trigger the construction of a new cell
- Construction rules are probabilistic

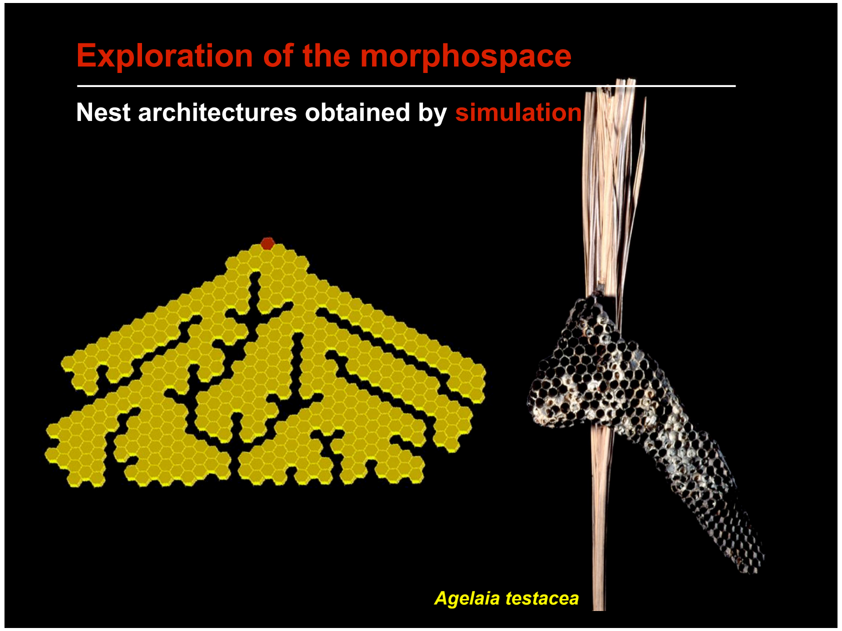
Simulations of collective building with a 3D lattice swarm

Nest architectures obtained by simulation

Polistes dominulus

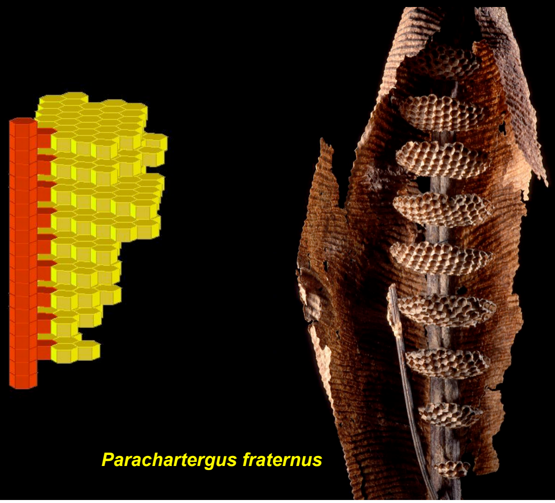



Exploration of the morphospace
Nest architectures obtained by simulation
Parapolybia varia


Exploration of the morphospace
Nest architectures obtained by simulation
Agelaia testacea

Exploration of the morphospace

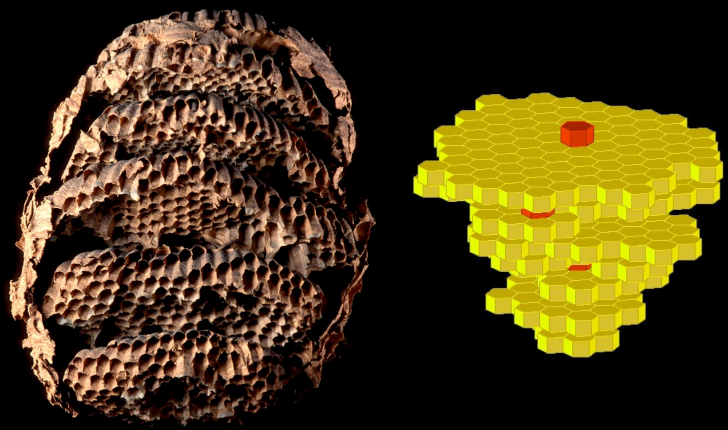
Nest architectures obtained by simulation



Parachartergus fraternus

Exploration of the morphospace

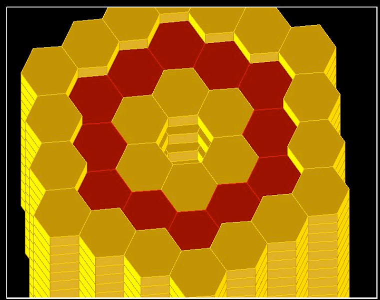
Nest architectures obtained by simulation



Vespa crabro

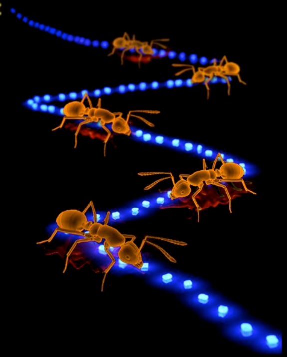
Exploration of the morphospace

Nest architectures obtained by simulation



Chartergus chartarius

Trail recruitment in ants : a stigmergic behavior

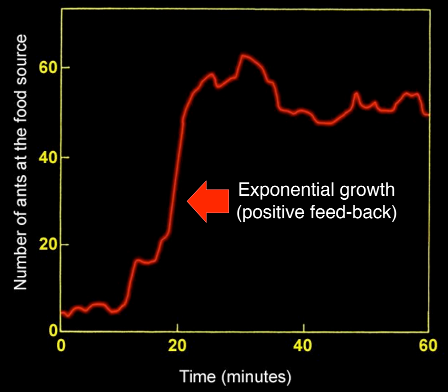


Ants looking for food: mass recruitment

Formation of foraging trails

- As the ants return from the food source to the nest, they lay down a trail of pheromones that can be followed other ants
- Recruited ants lay down their own pheromone on the trail as well, reinforcing the pathway
- Trail formation results from a positive feed-back

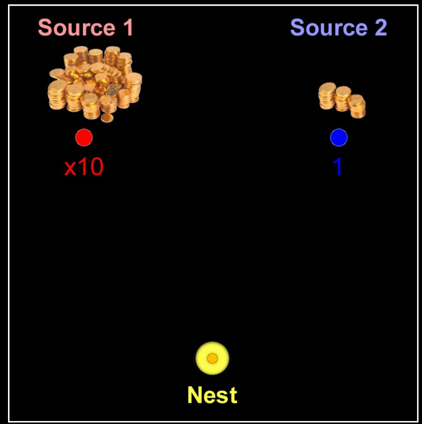
Amplifying communications

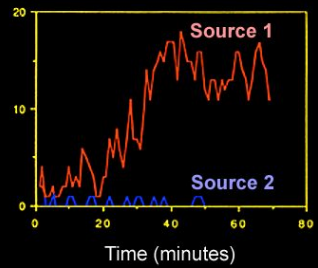


- Positive feed-back leads to an exponential growth of the number of ants at the food source superseded by a phase in which further growth is self-inhibited (all the available foragers have been recruited)
- Negative feed-back results from the evaporation of pheromone or the exhaustion of the food source
- Trail's recruitment system enables efficient decision making (e.g.: selection of the richest food source)

Collective decisions based on stigmergic interactions

The selection of the richest food source

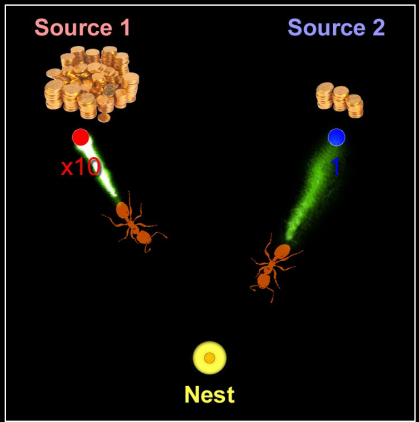




- None of ants visit both food sources
- Ants do not compare the richness of food sources to decide which one is the best

Collective decisions

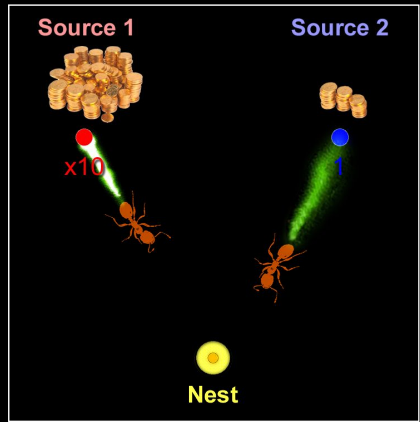
The selection of the richest food source



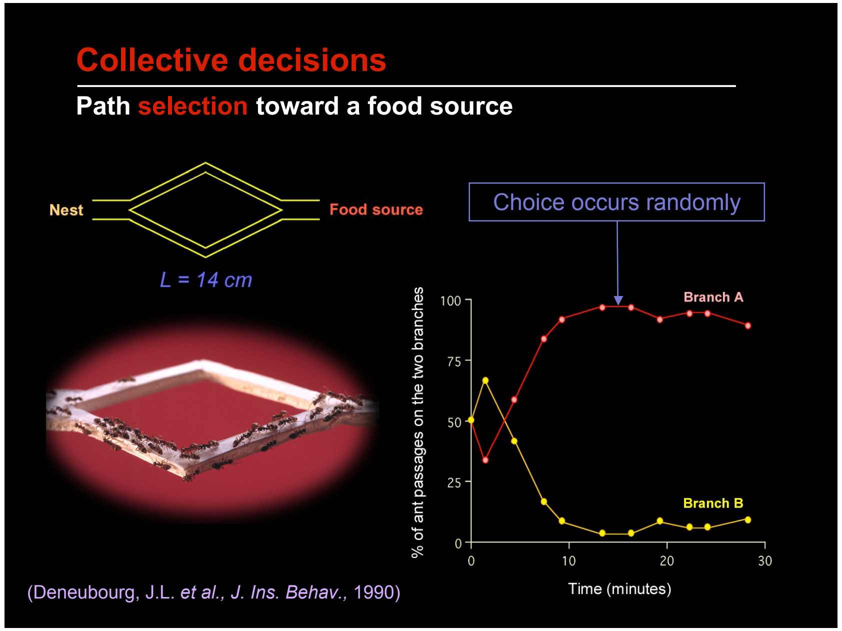
- Ants modulate the intensity of trail laying as a function of the quality of the food source by changing the frequency of marking

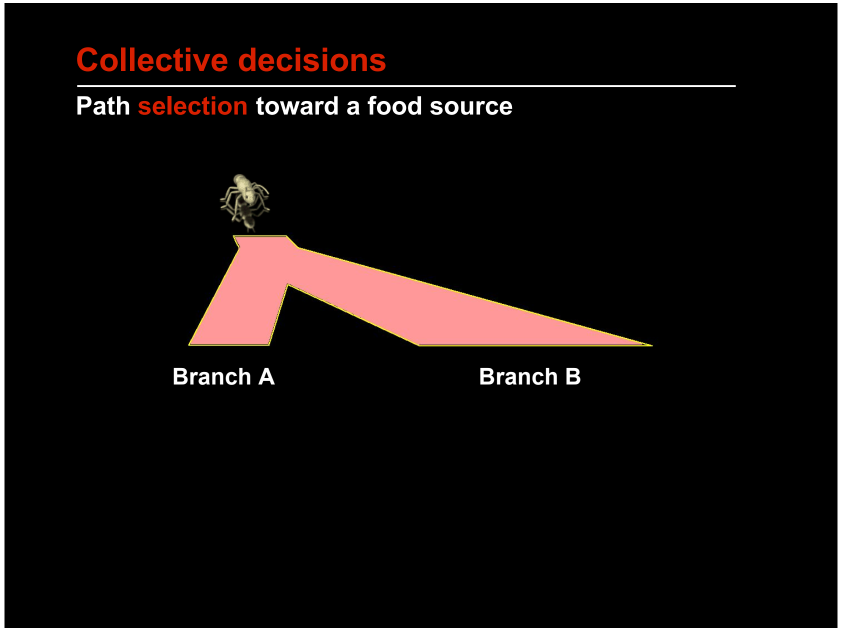
Collective decisions

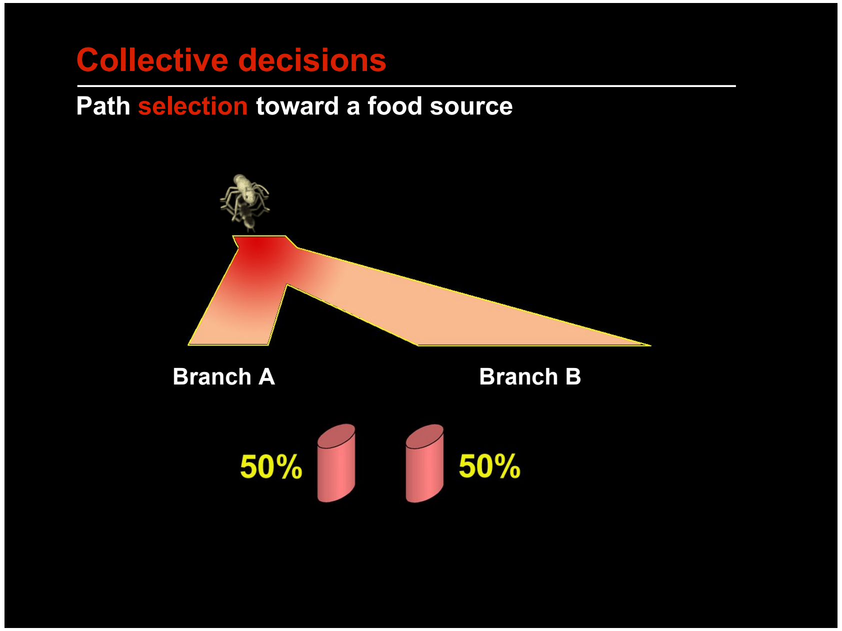
The selection of the richest food source

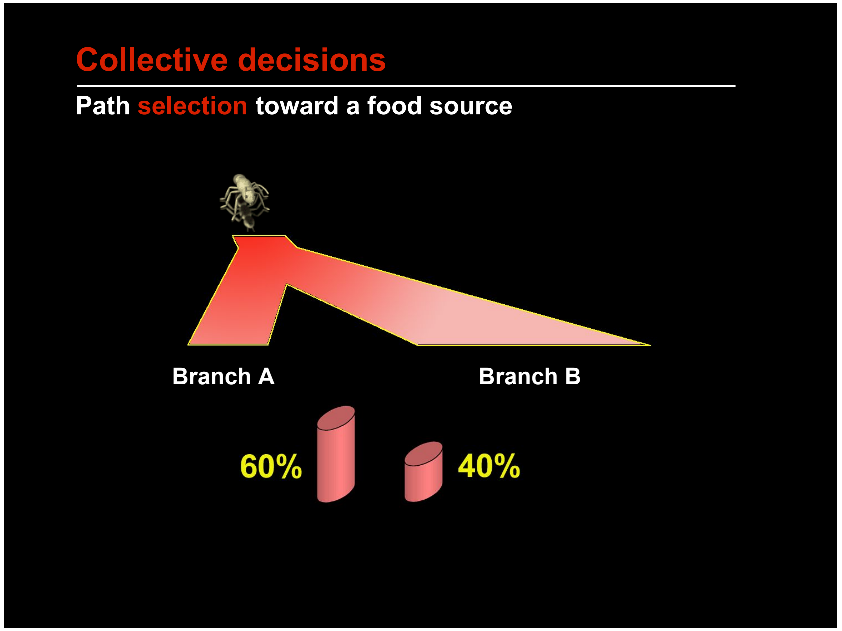


- Ants modulate the intensity of trail laying as a function of the quality of the food source by changing the frequency of marking
- The colony as a whole "chooses" the most rewarding source
- A simple trail-laying trail-following behavior enables a colony to make efficient collective choices without any sophisticated individual behavior


Collective decisions
Path selection toward a food source
Nest
Food source
L = 14 cm
Choice occurs randomly
% of ant passages on the two branches
100
75
50
25
0
0
10
20
30
Time (minutes)
Branch A
Branch B
(Deneubourg, J.L. et al., J. Ins. Behav., 1990)

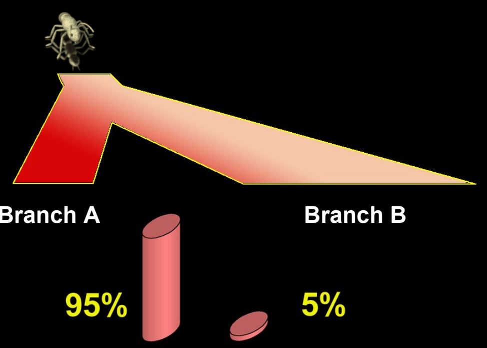

Collective decisions
Path selection toward a food source
Branch A
Branch B


Collective decisions
Path selection toward a food source
Branch A
Branch B
50%
50%


Collective decisions
Path selection toward a food source
Branch A
Branch B
60%
40%

Collective decisions

Path selection toward a food source



Modeling the collective decision

Model description

$$\mathrm{p}(C_i \mid C_1, C_2) = \frac{(k + C_i)^\alpha}{(k + C_1)^\alpha + (k + C_2)^\alpha} \quad , i = 1,2$$

Probability for an ant to choose branch C_i

$$\frac{dC_i}{dt} = \boxed{\Phi}\,\mathrm{p}(C_i \mid C_1, C_2) - \boxed{\mu}\, C_i \quad , i = 1,2$$

Dynamics of collective choice

C_1 , C_2 : concentrations in pheromone on branches 1 and 2

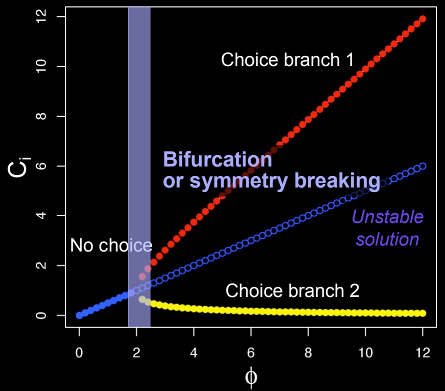
Φ : total flux of ants leaving the nest

μ : characteristic time of pheromone evaporation

Deneubourg, J.L. *et al., J. Ins. Behav.*, (1989)

Modeling the collective decision

Solutions of the model



Parameters' values

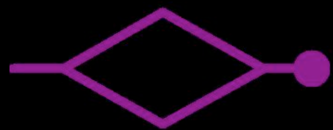
$\alpha = 2$
$k = 4$

- The incoming flux of ants leaving the nest is a bifurcation parameter that controls the collective behavior of the system
- A bifurcation that corresponds to qualitative changes in a system' s behavior is a key property of self-organized processes

Deneubourg, J.L. *et al., J. Ins. Behav.*, (1989)

Collective decisions

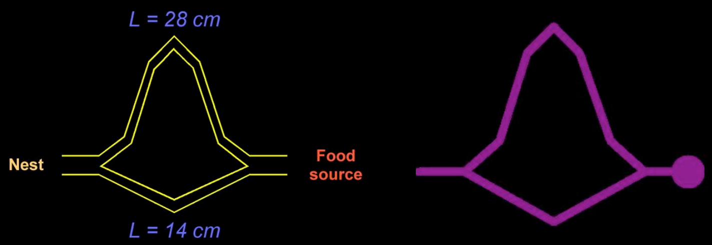
Path selection toward a food source



- Collective decisions in social insects arise through the competition among different types of information
- The trail that succeeds to grow faster will be selected, leading all the traffic to take place on one of the competing branches
- Environmental constraints interplay with the positive feedback

Collective decisions

Selection of the shortest route toward a food source

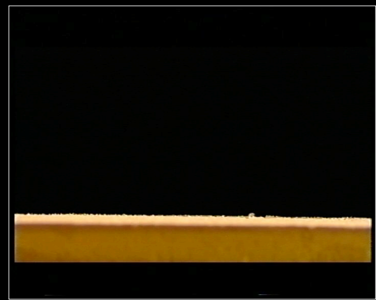


(Goss, S. *et al.*, *Naturwissenschaften*, 1989)

Collective decisions

Selection of the shortest route toward a food source

- Ants first use both paths in equal numbers, laying down pheromones as they move
- Ants taking the shorter path return to the nest faster
- The shorter path will then be doubly marked with pheromone, and will thus be more attractive
- Geometrical constraints play a key role in the collective decision-making processes that emerge at the colony level



Direct transmission of informations

Trophallactic
and antennal conatcts

Waggle dance

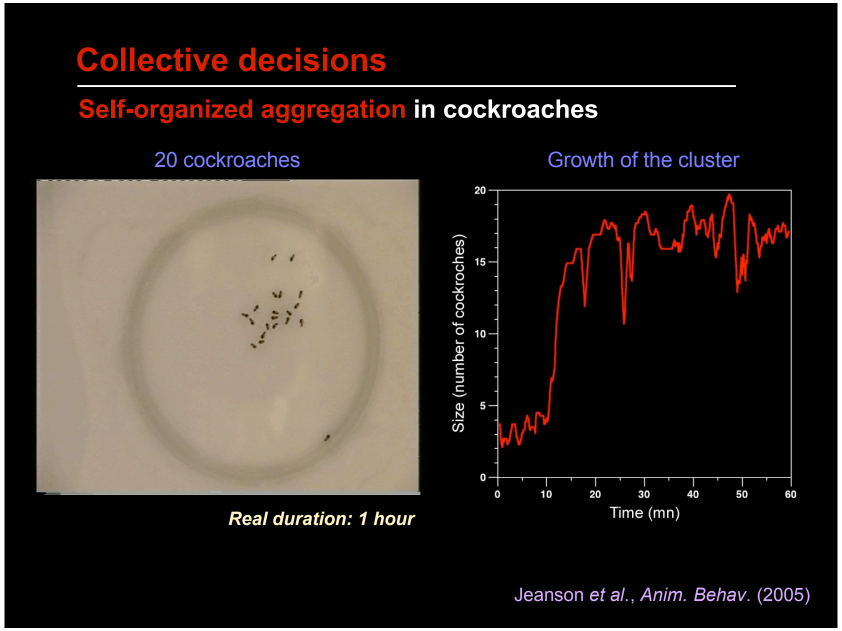
Apis mellifera

Collective decisions

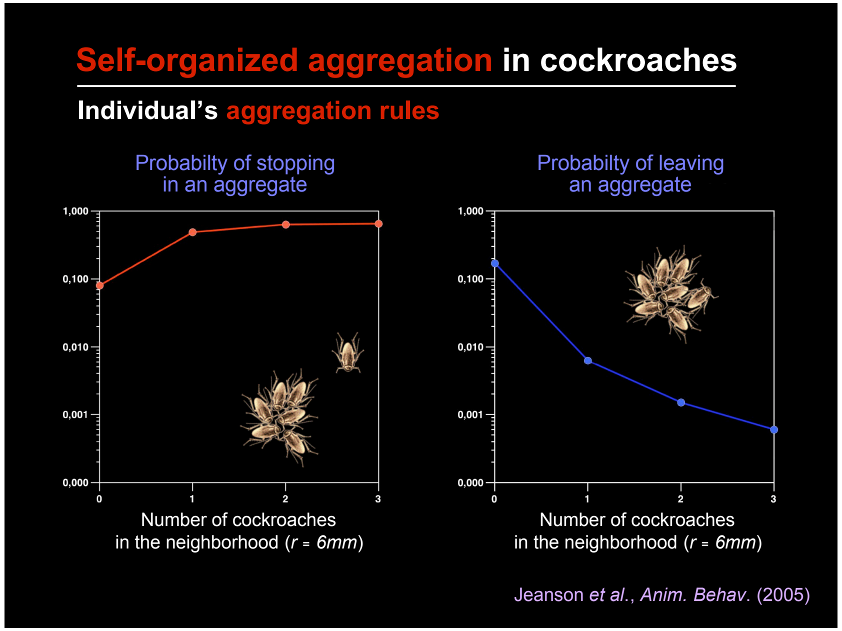
Self-organized aggregation in cockroaches

20 cockroaches

Real duration: 1 hour



Collective decisions
Self-organized aggregation in cockroaches
20 cockroaches
Growth of the cluster
Size (number of cockroaches)
Time (mn)
Real duration: 1 hour
Jeanson et al., Anim. Behav. (2005)

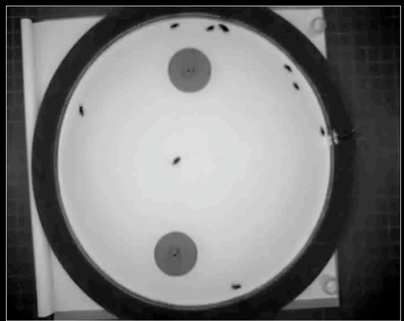


Self-organized aggregation in cockroaches
Individual's aggregation rules
Probabilty of stopping in an aggregate
Probabilty of leaving an aggregate
Number of cockroaches in the neighborhood (r = 6mm)
Number of cockroaches in the neighborhood (r = 6mm)
Jeanson et al., Anim. Behav. (2005)

Collective decisions

Collective choice of an aggregation site in cockroaches

Choice between 2 resting sites in
Periplaneta americana (10 cockroaches)



Real duration: 1 hour

- Cockroaches prefer dark places and avoid light: in a lighted arena cockroaches aggregate under the dark shelter
- When there are two identical dark shelters in the arena, cockroaches collectively choose to aggregate under only one of these shelters

Ame *et al.*, *Anim. Behav.* (2004)

Self-organization: a cornerstone for understanding collective behaviors

- Self-organization is a set of dynamical mechanisms whereby structures (nests, trail networks) or decisions (selection of a food source) emerge at the global level of a system from interactions among its lower-level components,
- Collective structures and decisions are not explicitly coded at the individual level

(Bonabeau, E. *et al.*, *TREE*, 1997)

The ingredients of self-organization

- Positive feedback (amplification): they are simple behavioral 'rules of thumb' that promote the creation of structures
- Negative feedback: counterbalances positive feedback and helps to stabilize the collective pattern: it may take the form of saturation, exhaustion or competition
- Amplification of fluctuations: fluctuations act as seeds from which structures nucleate and grow. Randomness enables the discovery of new solutions

(Bonabeau, E. *et al.*, *TREE*, 1997)

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- Amplification of fluctuations: fluctuations act as seeds from which structures nucleate and grow. Randomness enables the discovery of new solutions
- Multiple interactions: enable the stochastic nature of the underlying mechanisms to produce large and enduring structures

(Bonabeau, E. *et al.*, *TREE*, 1997)

Self-organized behaviors: a widely spread feature in biological systems

Sturnus vulgaris (© C. Carrere)

Bigeye jack (© D. Hall)

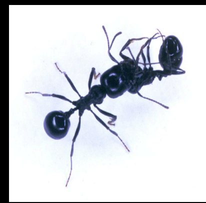
Homo sapiens

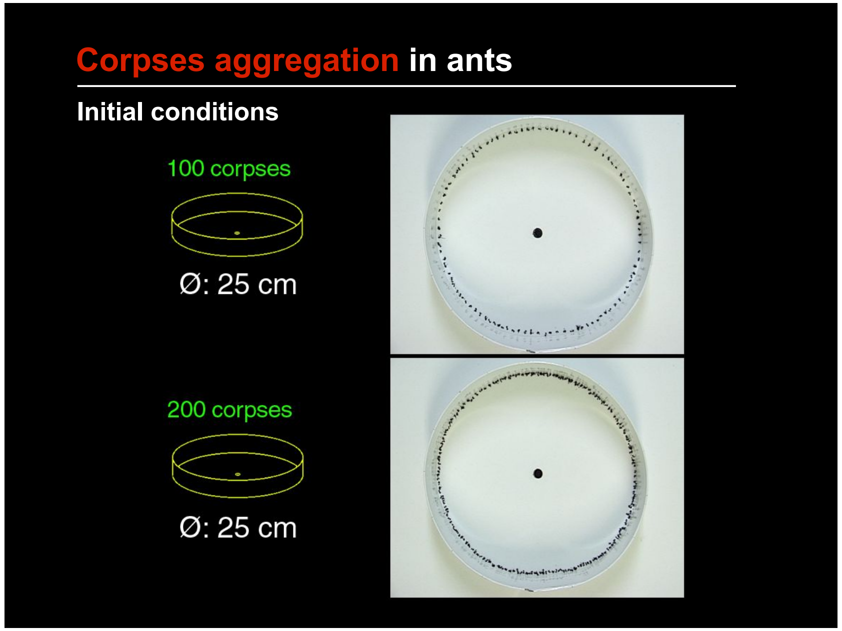
- Self-organization processes are found in a large number animal societies, from bacterial colonies to fish schools, herds of ungulates … to human groups

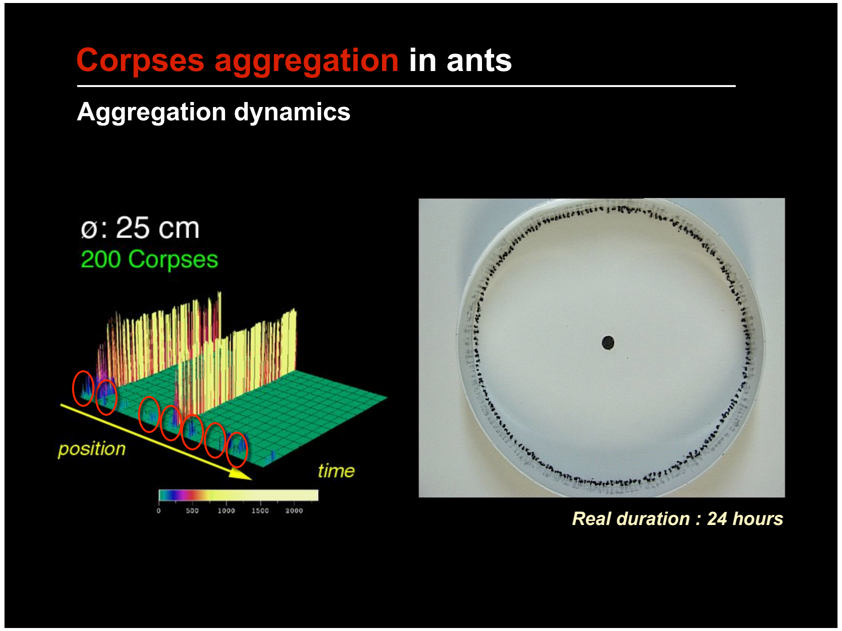
Properties of self-organization

Emergence of spatial patterns in an homogenous medium

Real duration : 36 hours

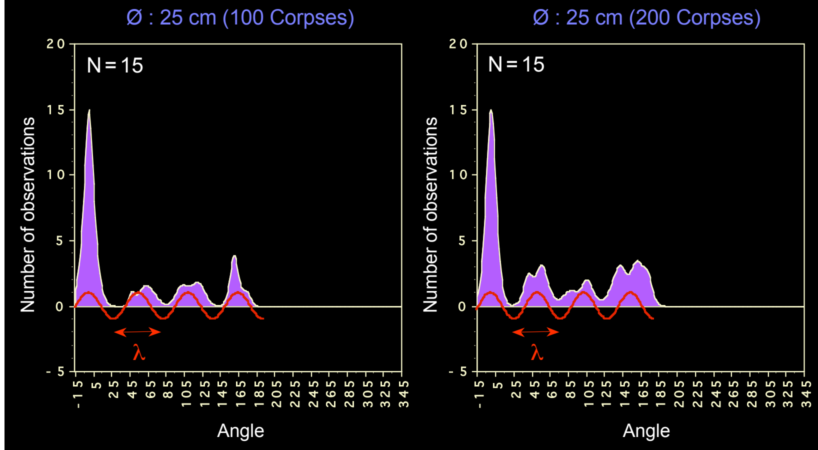



Corpses aggregation in ants
Initial conditions
100 corpses
Ø: 25 cm
200 corpses
Ø: 25 cm


Corpses aggregation in ants
Aggregation dynamics
ø: 25 cm
200 Corpses
position
time
Real duration : 24 hours

Corpses aggregation in ants

Spatial distribution of clusters after 24 hours



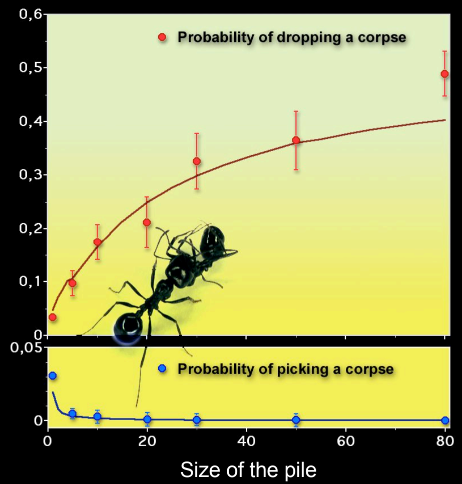
Corpses aggregation in ants

Range of perception of an ant

- The individual probabilities to pick-up and drop a corpse on a given cluster depend on the density of corpses which is perceived locally by the ant
- Experimental measurements lead to characteristic radius of perception $\Delta \approx$ 5mm

Corpses aggregation in ants

Picking-up and dropping behaviors



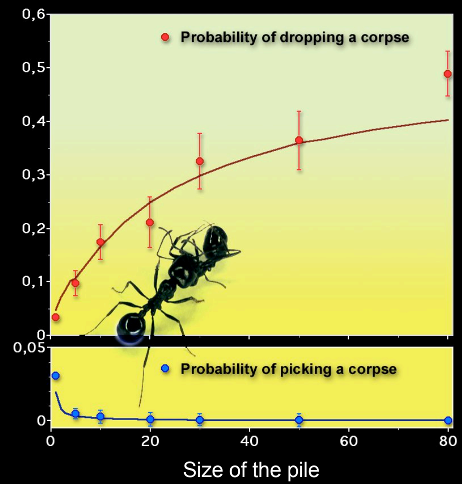
- Unladen ants pick up corpses with a probability that decreases with cluster size
- Corpse-carrying ants drop corpses with a probability that increases with cluster size

Positive feed-back

(Theraulaz, G. *et al.*, *PNAS*, 2002)

Corpses aggregation in ants

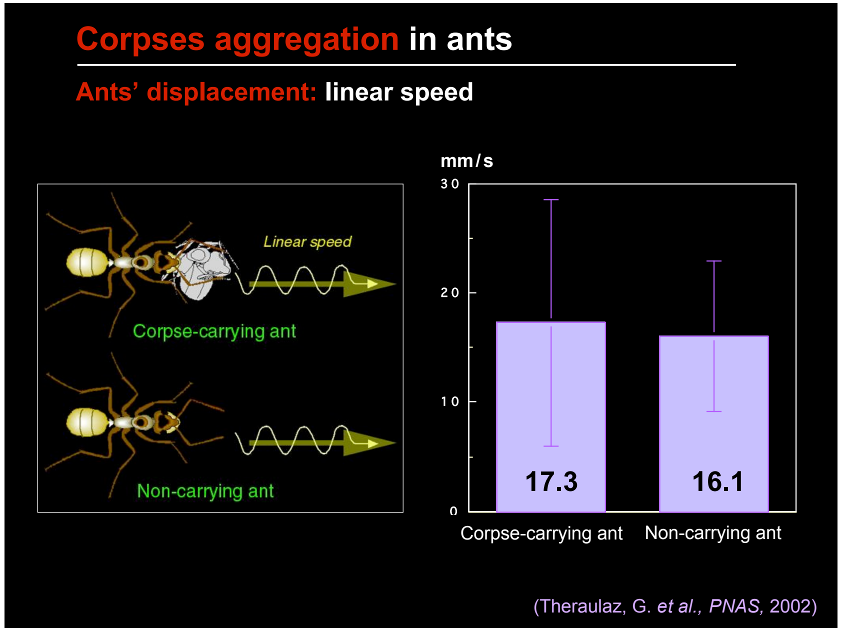
Picking-up and dropping behaviors

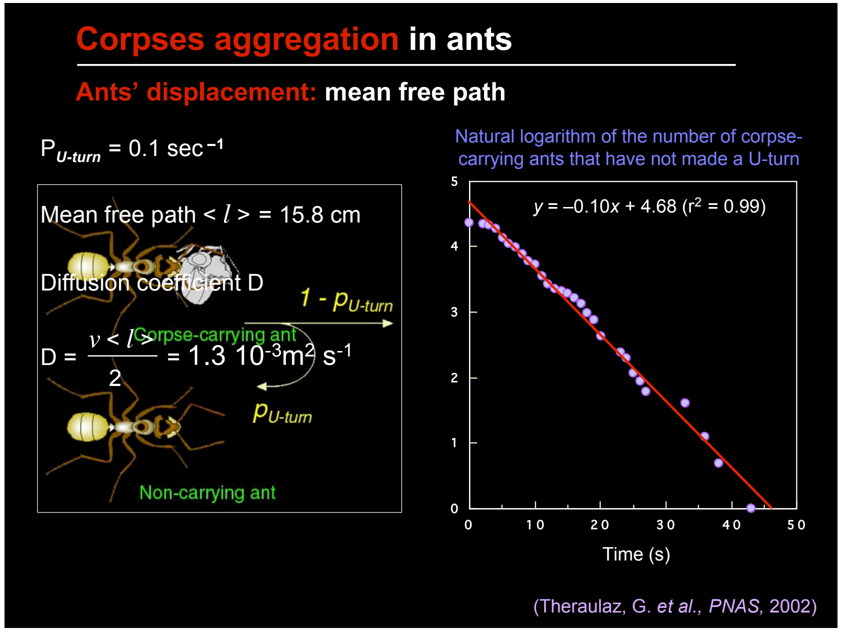


- Unladen ants pick up corpses with a probability that decreases with cluster size
- Corpse-carrying ants drop corpses with a probability that increases with cluster size
- The growth of clusters leads to a depletion of corpses in the arena that inhibits the further growth of other clusters

Negative feed-back

(Theraulaz, G. *et al.*, *PNAS*, 2002)


Corpses aggregation in ants
Ants' displacement: linear speed
Linear speed
Corpse-carrying ant
Non-carrying ant
mm/s
30
20
10
0
17.3
16.1
Corpse-carrying ant
Non-carrying ant
(Theraulaz, G. et al., PNAS, 2002)


Corpses aggregation in ants
Ants' displacement: mean free path
P U-turn = 0.1 sec −1
Mean free path < l > = 15.8 cm
Diffusion coefficient D
D = v < l > / 2 = 1.3 10-3m2 s-1
1 - pU-turn
Corpse-carrying ant
pU-turn
Non-carrying ant
Natural logarithm of the number of corpse-carrying ants that have not made a U-turn
y = –0.10x + 4.68 (r2 = 0.99)
5
4
3
2
1
0
0
10
20
30
40
50
Time (s)
(Theraulaz, G. et al., PNAS, 2002)

Reaction-diffusion model
of corpses aggregation in ants

Model description

Spontaneous dropping

Density of corpses $c(x,t)$

$$\frac{\partial c}{\partial t} = v\left[\boxed{k_d\, a} + \frac{\alpha_1 a\, \phi_C}{\alpha_2 + \phi_C} - \frac{\alpha_3\, \rho\, c}{\alpha_4 + \phi_C} \right]$$

Density of corpse-carrying ants $a(x,t)$

$$\frac{\partial a}{\partial t} = v\left[-k_d\, a - \frac{\alpha_1 a\, \phi_C}{\alpha_2 + \phi_C} + \frac{\alpha_3\, \rho\, c}{\alpha_4 + \phi_C} \right] + D\,\frac{\partial^2 a}{\partial x^2}$$

(Theraulaz, G. *et al.*, *PNAS*, 2002)

Reaction-diffusion model
of corpses aggregation in ants

Model description

Density-dependent dropping

Spontaneous dropping

Density-dependent picking-up

Diffusion

Density of corpses $c(x,t)$

$$\frac{\partial c}{\partial t} = v\left[\boxed{k_d\, a} + \boxed{\frac{\alpha_1 a\, \phi_C}{\alpha_2 + \phi_C}} - \boxed{\frac{\alpha_3\, \rho\, c}{\alpha_4 + \phi_C}} \right]$$

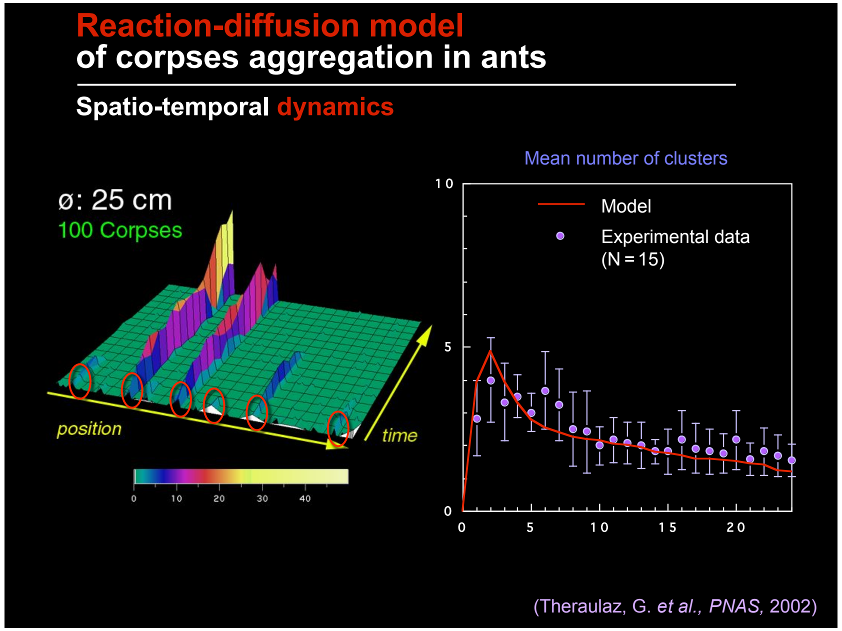
Density of corpse-carrying ants $a(x,t)$

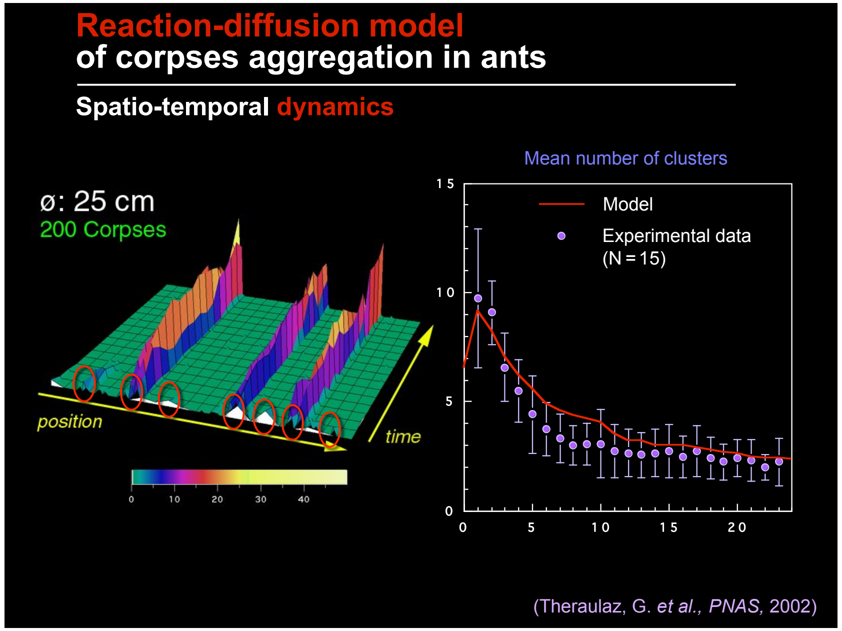
$$\frac{\partial a}{\partial t} = v\left[-k_d\, a - \frac{\alpha_1 a\, \phi_C}{\alpha_2 + \phi_C} + \frac{\alpha_3\, \rho\, c}{\alpha_4 + \phi_C} \right] + \boxed{D\,\frac{\partial^2 a}{\partial x^2}}$$

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

Local density of corpses perceived by an ant

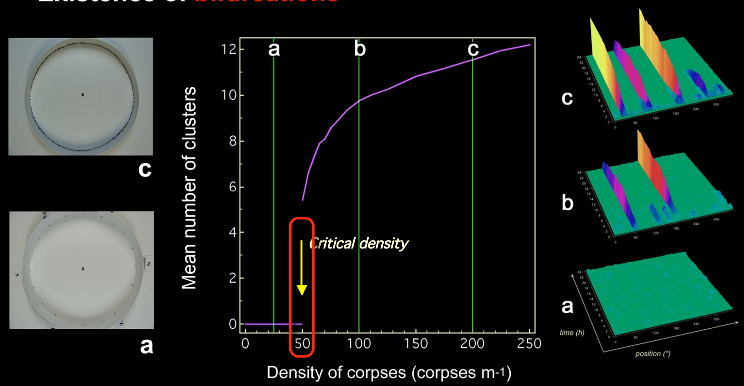
(Theraulaz, G. *et al.*, *PNAS*, 2002)


Reaction-diffusion model
of corpses aggregation in ants
Spatio-temporal dynamics
ø: 25 cm
100 Corpses
position
time
Mean number of clusters
Model
Experimental data
(N = 15)
(Theraulaz, G. et al., PNAS, 2002)


Reaction-diffusion model
of corpses aggregation in ants
Spatio-temporal dynamics
ø: 25 cm
200 Corpses
position
time
Mean number of clusters
Model
Experimental data
(N = 15)
(Theraulaz, G. et al., PNAS, 2002)

Reaction-diffusion model
of corpses aggregation in ants

Existence of bifurcations

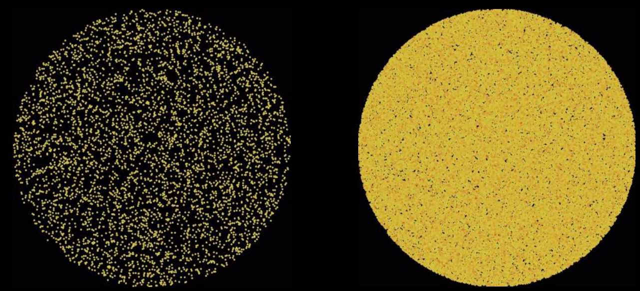


- The density of corpses is a bifurcation parameter that controls the collective behavior of the system : there exists a critical density of corpses below which no aggregation occurs

Reaction-diffusion model
of corpses aggregation in ants

2D Monte Carlo simulation

Low density ➡ clusters High density ➡ sponge-like structures



Ø : 50 cm
5000 Corpses

Ø : 50 cm
80000 Corpses

- Under different initial conditions, the same behavioral rules at the individual level lead to the formation of different patterns

(Theraulaz, G. *et al.*, *Phil. Trans. R. Soc. Lond. B*, 2003)

Architectures without architects

Lasius niger

Properties of self-organization

Multi-stability

Diameter of the arena: 25cm
200 corpses

Real duration : 24 hours

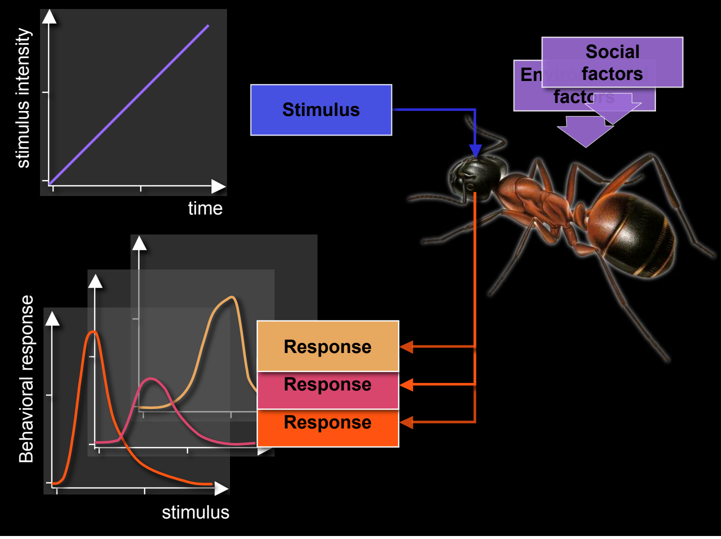
Diameter of the arena: 25cm
200 corpses

Real duration : 24 hours

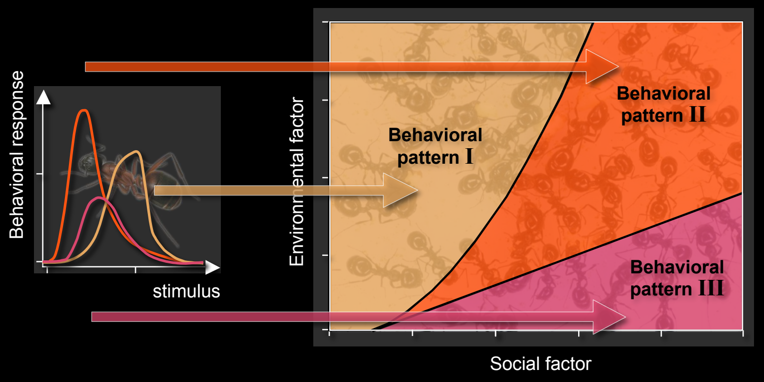
- Self-organized systems are multi-stable : for a given set of parameters, the system can reach different stable states depending on the initial conditions and on the random fluctuations

The modulation of self-organized behaviors

The modulation of self-organized behaviors



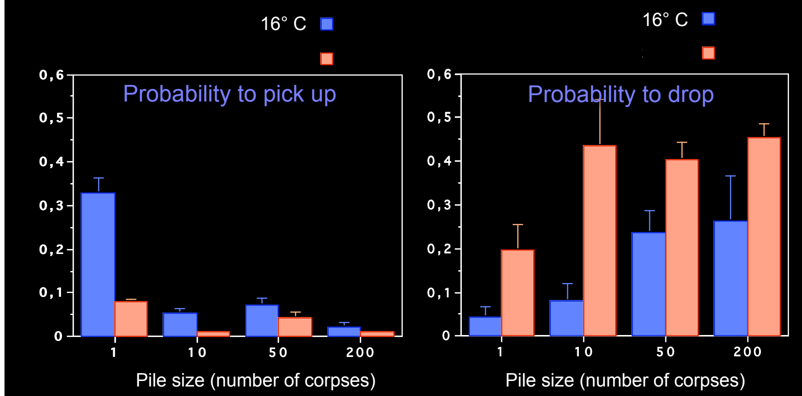
The modulation of self-organized behaviors



- The modulation of the individual behavior by environmental (e.g.: temperature level, wind speed …) and social factors (colony size, caste ratio …) shape the properties that emerge at the collective level

The modulation of self-organized behaviors

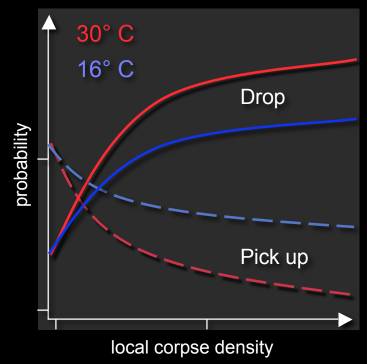
Effect of temperature on picking up and dropping behaviors

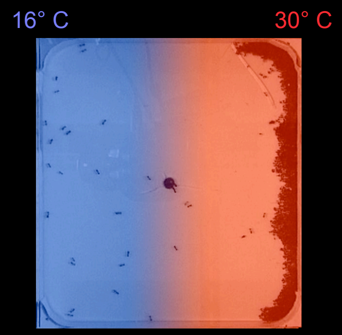


(Challet *et al.*, *Insectes Soc.*, 2005)

The modulation of self-organized behaviors

Effect of temperature on spatio-temporal clustering dynamics



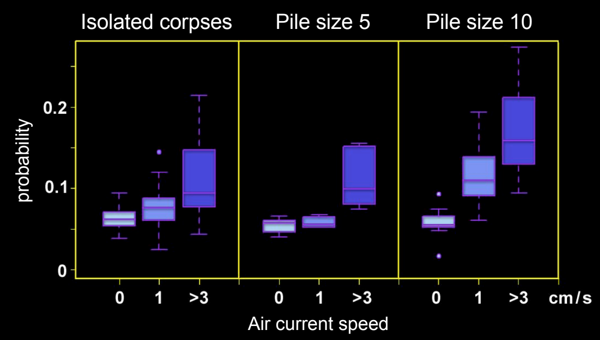


Real duration : 24 hours

- Positive feed-back is stronger at 30° C than at 16° C
- Corpse are clustered in the warmest area of the setup

The modulation of self-organized behaviors

Effect of wind speed on picking up behavior

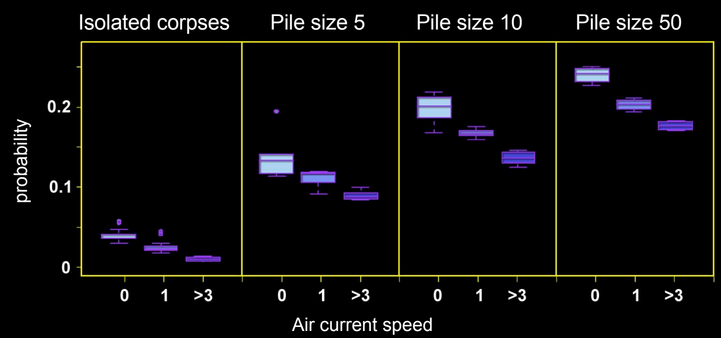


- Pick up probability increases with wind speed

(Jost *et al.*, *J. Roy. Soc. Interface*, 2007)

The modulation of self-organized behaviors

Effect of wind speed on dropping behavior

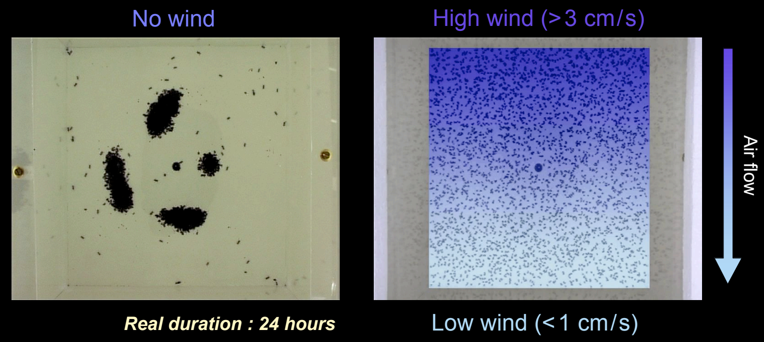


- Dropping probability decreases with wind speed
- Ants clear corpses from areas of high wind speed and aggregate them in areas of low wind speed

(Jost *et al.*, *J. Roy. Soc. Interface*, 2007)

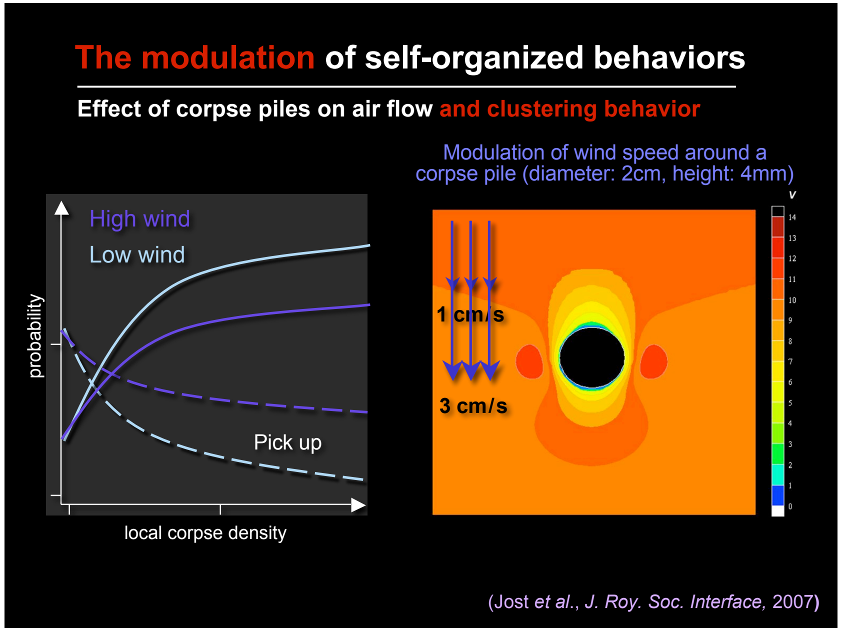
The modulation of self-organized behaviors

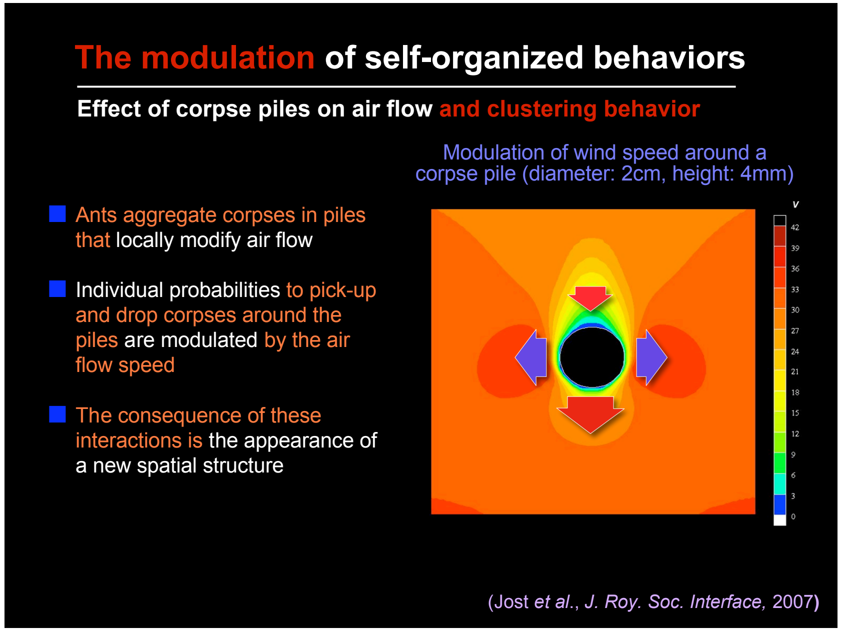
Effect of wind on spatio-temporal clustering dynamics



- Positive feed-back is stronger in low wind zones
- Clusters form in the low wind zone and are elongated in the direction of the air flow

(Jost *et al.*, *J. Roy. Soc. Interface*, 2007)


The modulation of self-organized behaviors
Effect of corpse piles on air flow and clustering behavior
Modulation of wind speed around a corpse pile (diameter: 2cm, height: 4mm)
High wind
Low wind
probability
Pick up
local corpse density
1 cm/s
3 cm/s
v
(Jost et al., J. Roy. Soc. Interface, 2007)

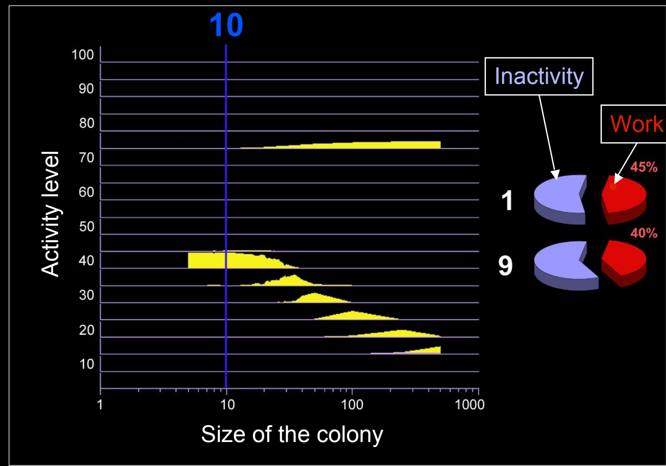

The modulation of self-organized behaviors
Effect of corpse piles on air flow and clustering behavior
Modulation of wind speed around a corpse pile (diameter: 2cm, height: 4mm)
Ants aggregate corpses in piles that locally modify air flow
Individual probabilities to pick-up and drop corpses around the piles are modulated by the air flow speed
The consequence of these interactions is the appearance of a new spatial structure
v
(Jost et al., J. Roy. Soc. Interface, 2007)

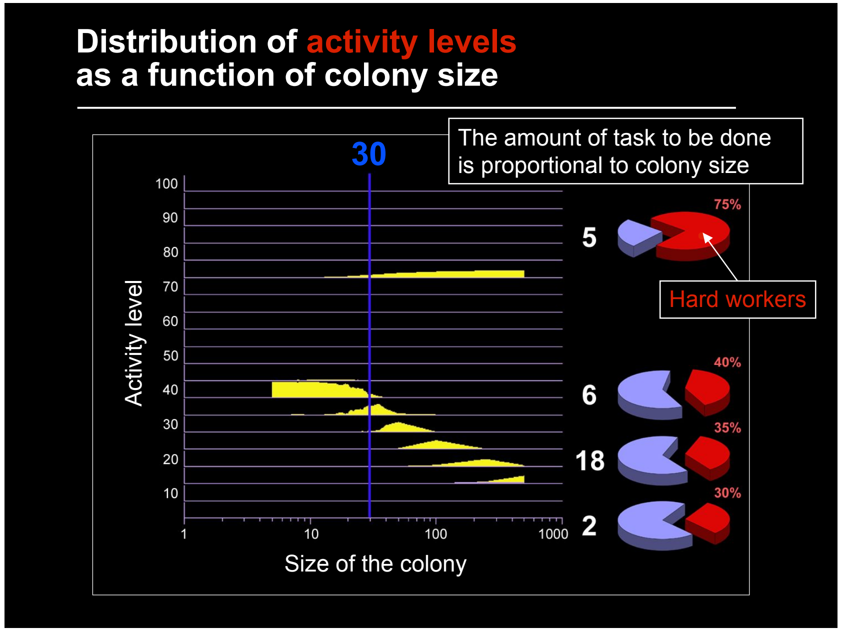
The modulation of self-organized behaviors

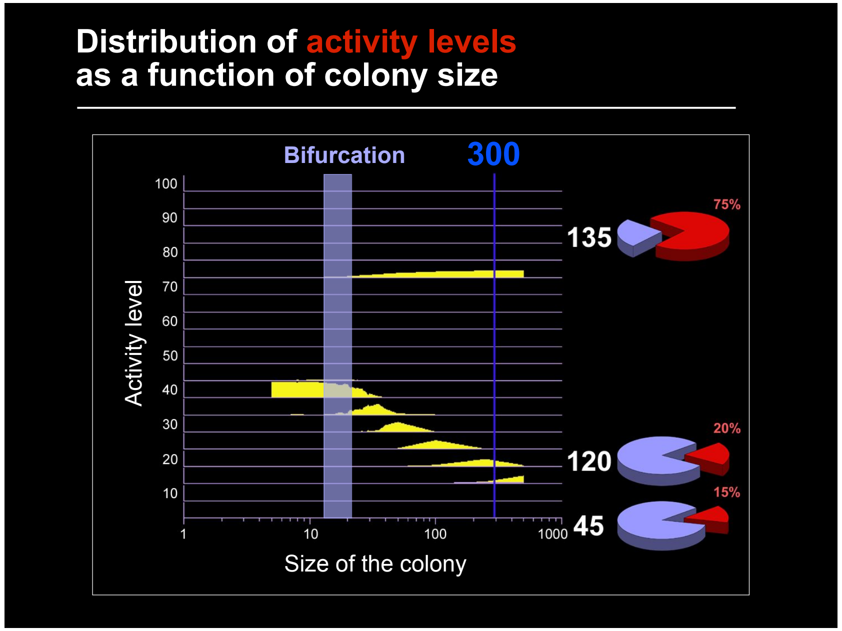
Effect of colony size on the division of labor in Polistes wasps

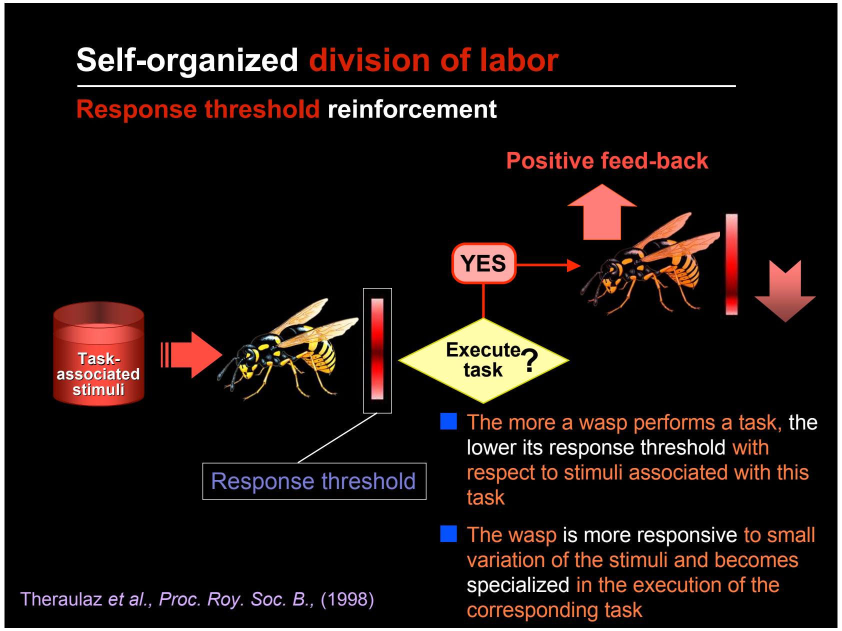
Polistes dominulus

Distribution of activity levels as a function of colony size

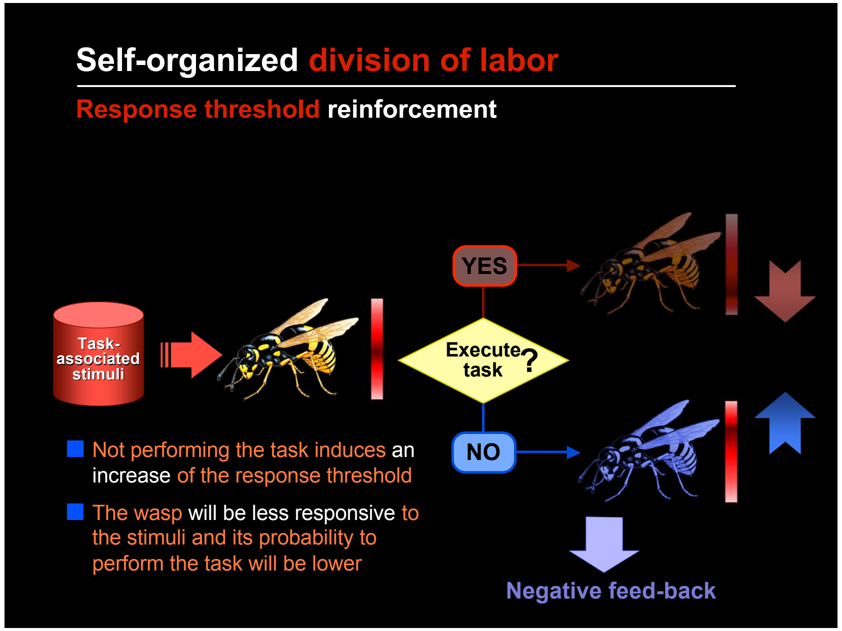



Distribution of activity levels
as a function of colony size
The amount of task to be done
is proportional to colony size
30
Hard workers
Activity level
Size of the colony
5
6
18
2
75%
40%
35%
30%

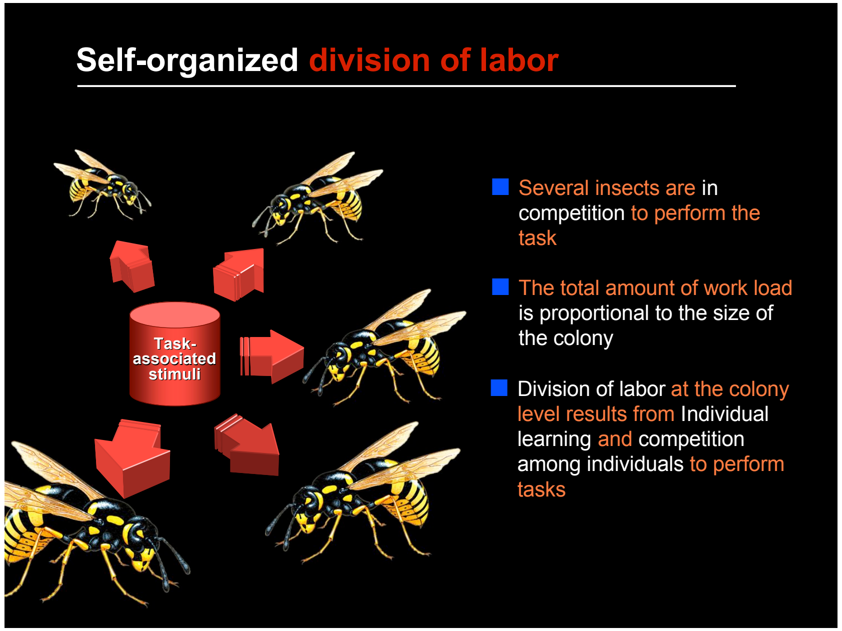

Distribution of activity levels
as a function of colony size
Bifurcation
300
Activity level
Size of the colony
135
120
45
75%
20%
15%

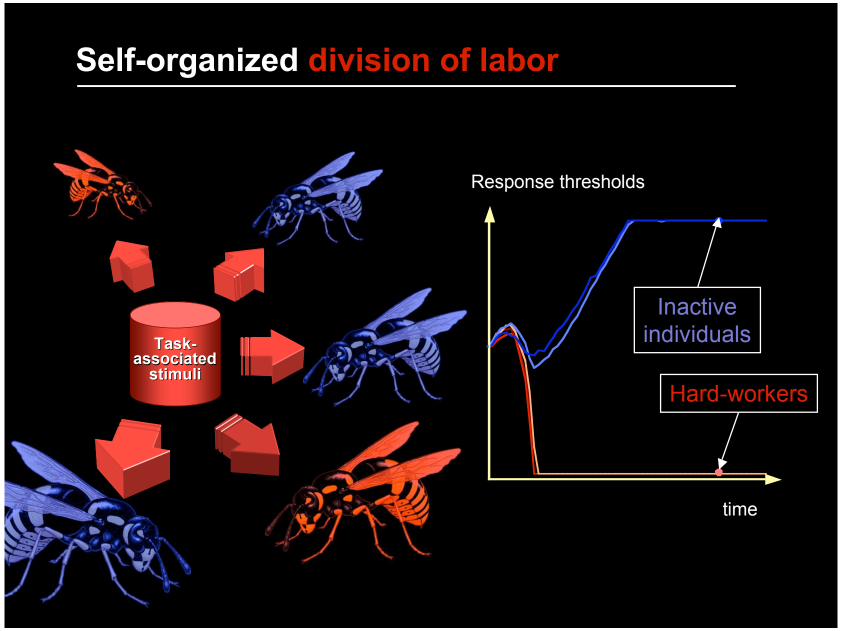


Self-organized division of labor
Response threshold reinforcement
Positive feed-back
YES
Execute task ?
Task-associated stimuli
Response threshold
The more a wasp performs a task, the lower its response threshold with respect to stimuli associated with this task
The wasp is more responsive to small variation of the stimuli and becomes specialized in the execution of the corresponding task
Theraulaz et al., Proc. Roy. Soc. B., (1998)



Self-organized division of labor
Response threshold reinforcement
YES
Execute task ?
NO
Task-associated stimuli
Not performing the task induces an increase of the response threshold
The wasp will be less responsive to the stimuli and its probability to perform the task will be lower
Negative feed-back


Self-organized division of labor
Task-associated stimuli
Several insects are in competition to perform the task
The total amount of work load is proportional to the size of the colony
Division of labor at the colony level results from Individual learning and competition among individuals to perform tasks


Self-organized division of labor
Task-associated stimuli
Response thresholds
Inactive individuals
Hard-workers
time

Self-organized division of labor

Activity level

10 wasps

30 wasps

300 wasps

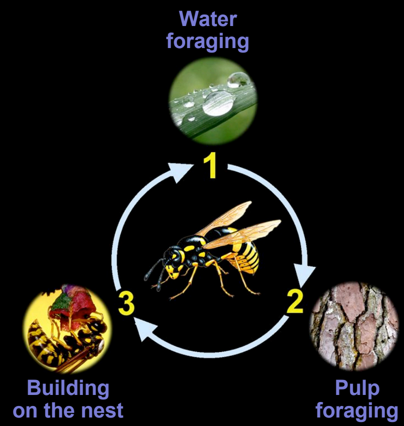
- In a small colony, the amount of work to be done is small and large fluctuations of work load occur with time: wasps have not enough time and no opportunity to undergo a differentiation
- As colony size is increasing, the absolute value of the amount of work to be done increases, fluctuations of task associated stimuli become weaker and greater are the chance for some individuals to become hard-workers

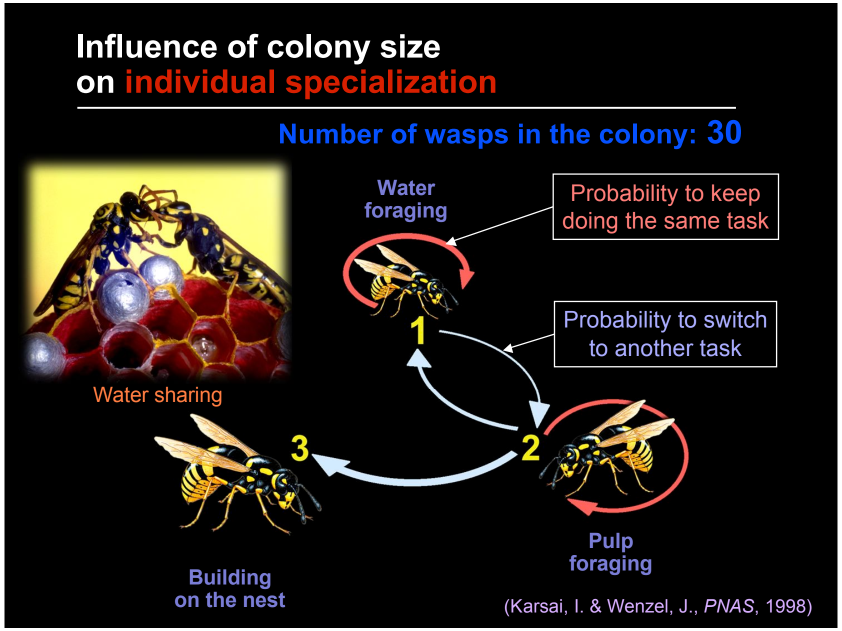
Gautrais *et al., J. theor. Biol.*, (2002)

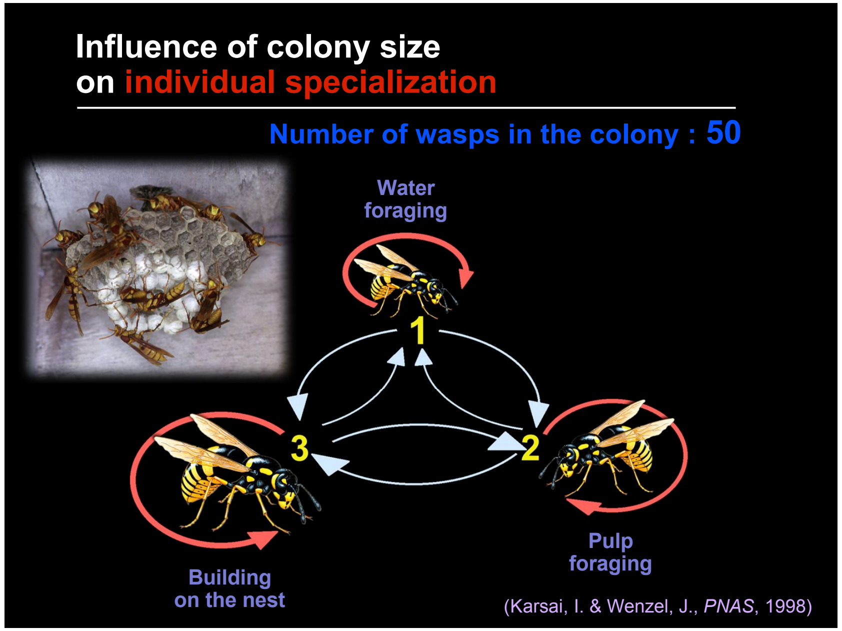
Sequence of tasks involved in nest construction

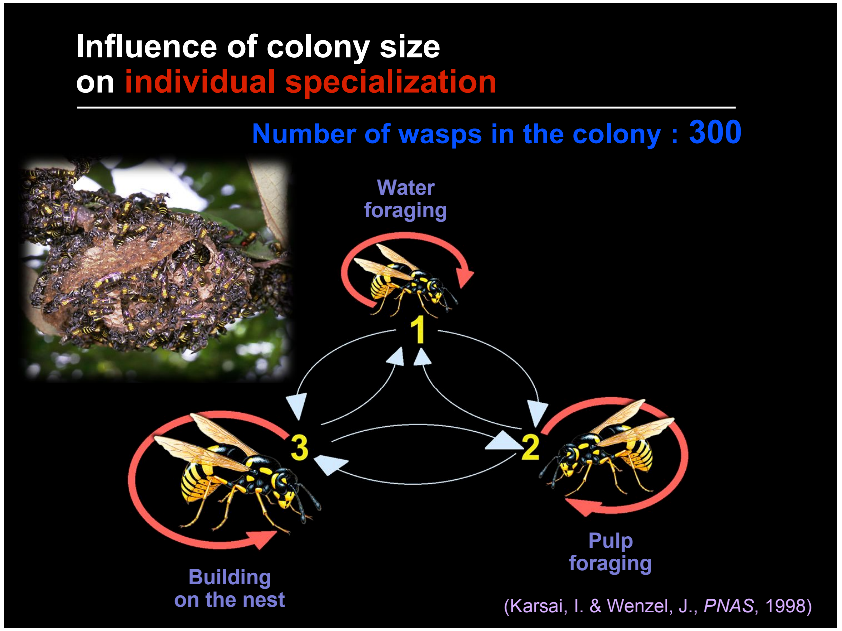
Polistes dominulus

- As colony size increases, individuals become specialized in performing tasks




Influence of colony size
on individual specialization
Number of wasps in the colony: 30
Water foraging
Probability to keep doing the same task
Probability to switch to another task
Water sharing
1
2
3
Pulp foraging
Building on the nest
(Karsai, I. & Wenzel, J., PNAS, 1998)

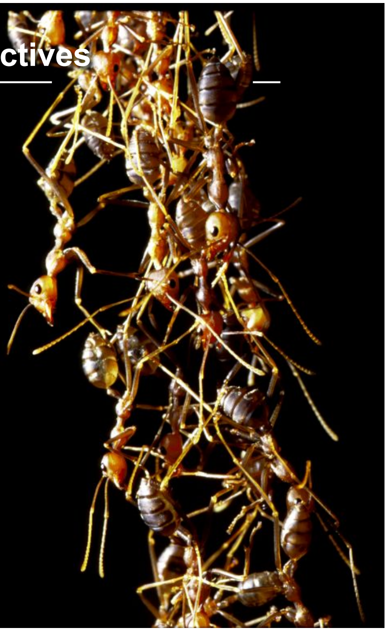

Influence of colony size
on individual specialization
Number of wasps in the colony : 50
Water foraging
1
2
3
Pulp foraging
Building on the nest
(Karsai, I. & Wenzel, J., PNAS, 1998)


Influence of colony size
on individual specialization
Number of wasps in the colony : 300
Water
foraging
1
2
3
Pulp
foraging
Building
on the nest
(Karsai, I. & Wenzel, J., PNAS, 1998)


The modulation of self-organized behaviors
Self-organized optimization of division of labor
The organization of division of labor is adapted to the size of the colony
In a large colony, with high work load, specialized, highly skilled workers increase the efficiency of the division of labor
Its is better for a small colony to keep generalist workers
Self-organization allows for the optimization of the division of labor

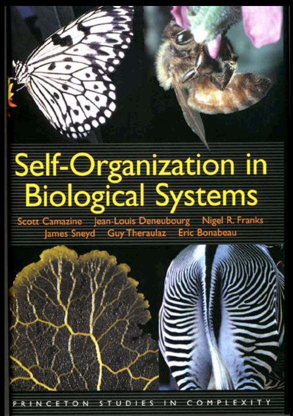
Conclusions and perspectives

- Complex colony-level structures and swarm intelligence of social insects emerge from decentralized interactions among individuals
- Self-organized patterns are flexible and robust
- Stigmergic behaviors can generate a huge variety of patterns and decisions in combination with environmental templates
- The modulation of individual rules increases the flexibility and the richness of the collective behaviors

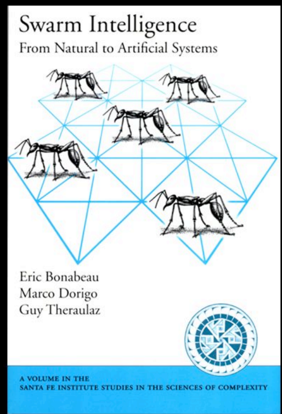


End of the road …

To learn more about self-organization and swarm intelligence in social insects



(Camazine *et al.*, 2001)
Princeton University Press



(Bonabeau, Dorigo & Theraulaz, 1999)
Oxford University Press