

# In the beginning there were chemicals



Patrizia d'Ettorre

Centre for Social Evolution, Department of Biology, University of Copenhagen, Denmark  
Laboratory of Experimental and Comparative Ethology, University of Paris 13, France

[pdettorre@bio.ku.dk](mailto:pdettorre@bio.ku.dk)



“Imagine a world in constant darkness and silence,  
but full of odors and tastes.

You are alarmed, soothed, and told what to do by scent,  
and by their perfumes you recognize the standing of those you interact  
with, what role they play in the society, and whether or not they belong  
to your family or work group.

This is life in an ant society, a *superorganism*

in which all communication is honest, free of deceit, and for the  
good of the group – **or is it?**”

The Journal of Experimental Biology 212, 1775-1779  
Published by The Company of Biologists 2009  
doi:10.1242/jeb.015008

## Commentary

### Honest and dishonest communication in social Hymenoptera

J. Heinze<sup>1,\*</sup> and P. d'Ettorre<sup>2</sup>

# Modes of communication

- Acoustic
- Visual
- Tactile

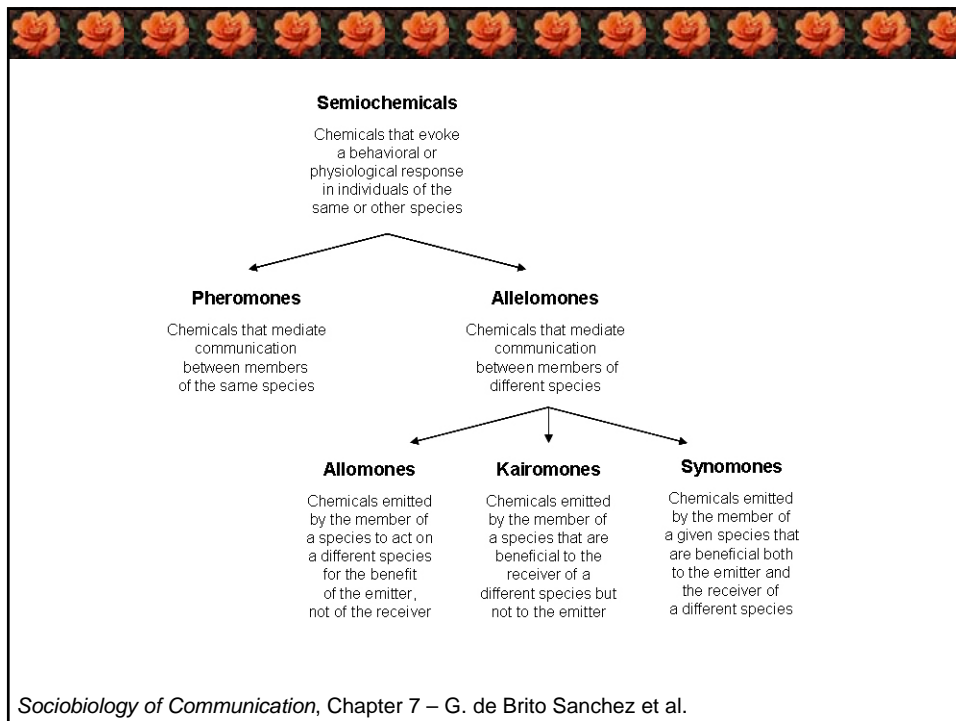
- **Chemical**



*Semiochemical* → substance used in communication

*Pheromone* (within species)

*Allelomone* (across species)



# Pheromones

**Original definition:** “substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific action” (Karlson and Lüscher 1959).

- From Chapter 5 *Sociobiology of Communication*:

**Broad definition** of Wyatt (2003), which includes olfactory and contact chemoreception, substances that are transferred directly from signaller to receiver and chemical cues used in social recognition (e.g. cuticular hydrocarbon patterns in insects). It is particularly important to note that we will refer to pheromones to both describe **cues** and **signals**.

## Chemical communication in social insects

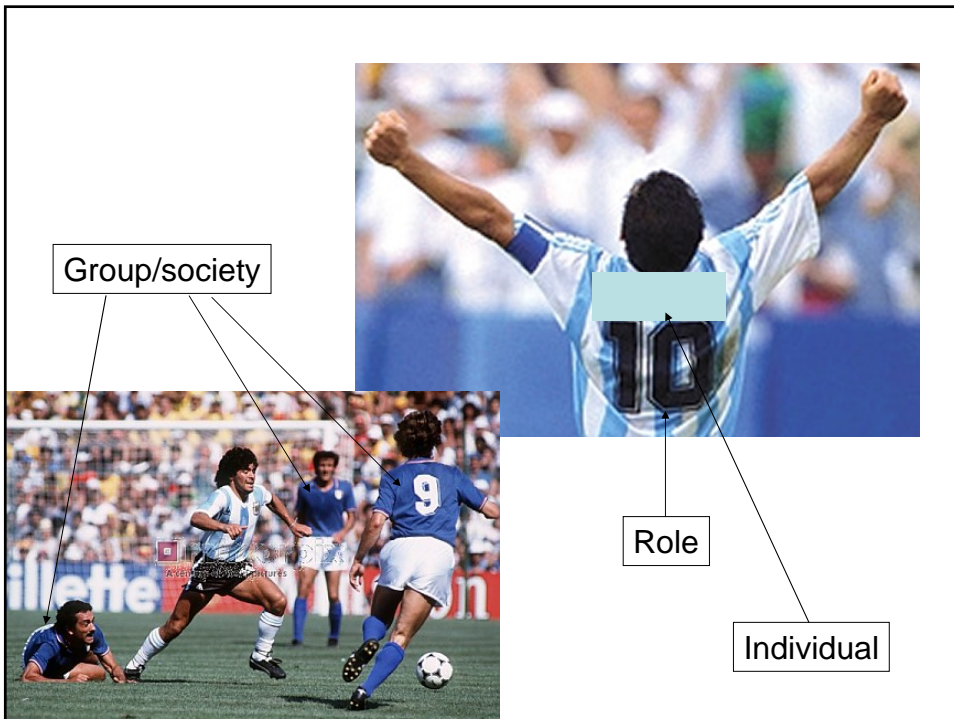
what for?

- Alarm
- Attraction
- Recruitment (food or nest site)
- Grooming
- Trophallaxis (exchange of oral or anal liquid)
- Exchange of solid food
- Caste determination
- Territorial signals and nest markers
- Sexual communication
- ....
- **Recognition**



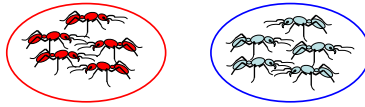
Photo: Daniel Kronauer

Who is who?

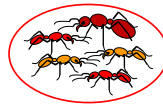


## Communication of identity in ants *levels of recognition*

inter-colony  
nestmate recognition



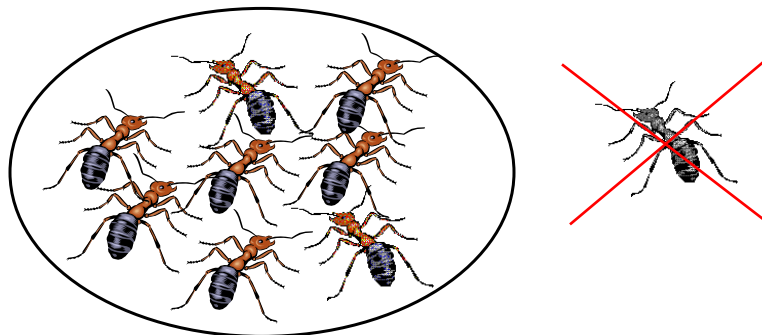
intra-colony  
within-colony recognition



inter-individual  
individual recognition



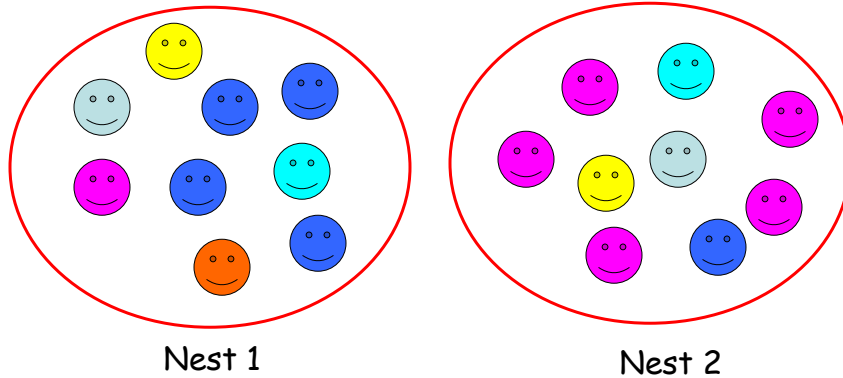
## Insect societies are generally closed



**Nestmate recognition is  
fundamental for social organisation**

## Nestmate recognition and Kin recognition are two different phenomena

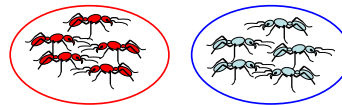
Mixed colonies



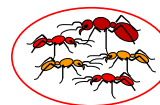
Same colour = kin

## Kin versus nestmate recognition in social insects

**Nestmate recognition** is discrimination **between** colony members and aliens. This is essential for the organization of insect societies since it prevents robbery and parasitism from outside



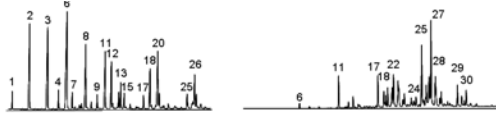
**Kin recognition** could take place **within** the colony, because the degrees of relatedness among nestmates can vary due to polyandry, polygyny or both.



*Kin and nestmate recognition coincide in social insects only when colonies are headed by a single queen, singly mated and there is no queen turn-over*

## How can recognition be possible anyway?

For recognition to occur  
individuals must be different



Cue diversity is expression of genetic variation



Polymorphism of genetic markers

**If there is a cost for being rejected**

Individuals with ~~rare~~ labels suffer high costs

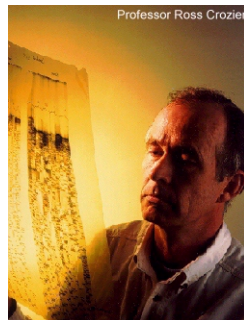
Individuals with common labels suffer low costs



All individuals in a population will carry the same genetic markers  
**Recognition is impossible!**

## But recognition is possible!

### The Crozier' paradox



Crozier 1987

## Mechanisms of recognition

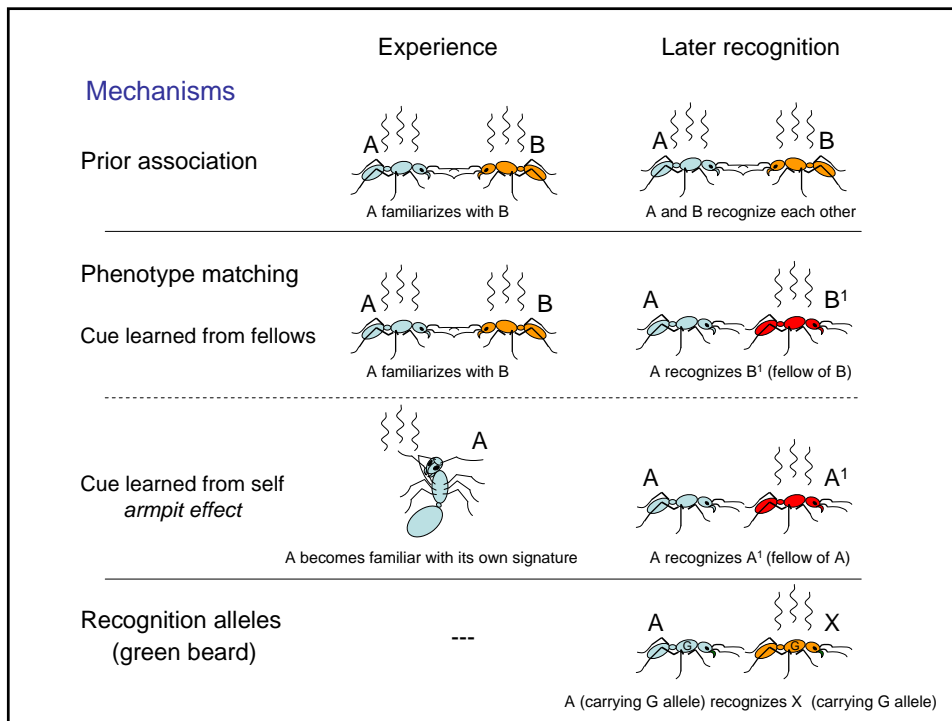
### *Indirect* recognition

the evaluator relies on some contextual cues (e.g. spatial location)

### *Direct* recognition

based on phenotypic cues that are actually borne by individuals

- Prior association
- Phenotype matching
- Recognition alleles (green beard)

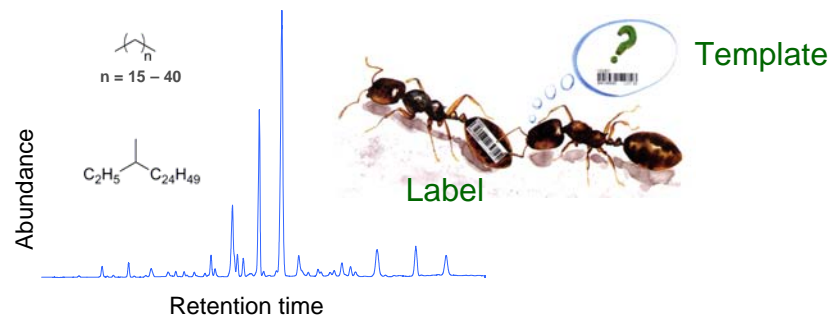




## Recognition cues

- In ants recognition cues are chemicals

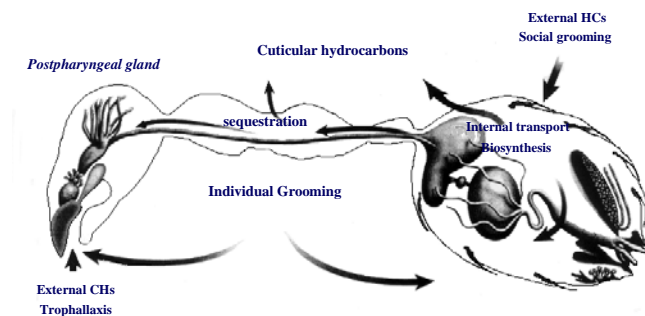
**Cuticular hydrocarbons** are considered to be the chemical cues responsible for recognition (label)



## Nestmate recognition cues

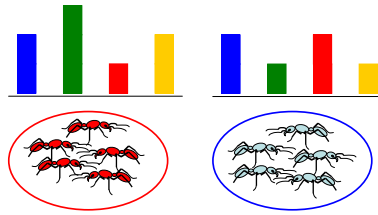
Nestmates share a common colony odour – *Gestalt model* (Crozier and Dix 1979)

The colony odour is not the simple sum of cues of the different individuals, but it is a new configuration, a pattern of elements resulting into a unified whole (*Gestalt*)



## Levels of recognition in ants

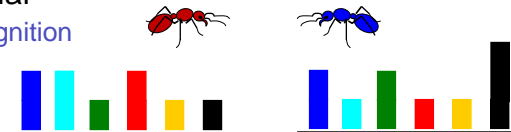
inter-colony  
nestmate recognition



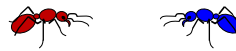
intra-colony  
within-colony recognition



inter-individual  
individual recognition



inter-individual  
individual recognition



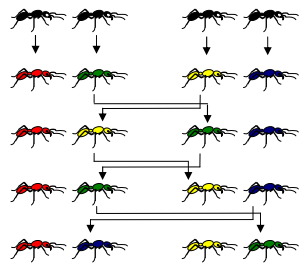
*Pachycondyla villosa*  
and *P. inversa*

- Queens associate to found a new colony
- They establish a rank order regulating the division of labour

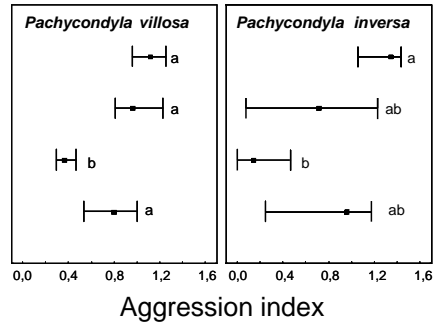
Dominance hierarchy:

- low ranking queens forage
- high ranking queens stay in the nest and care the brood

In *Pachycondyla villosa* and *P. inversa*  
Individual recognition occurs  
and it involves long term memory of individual identity



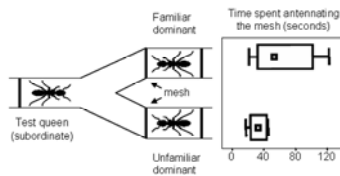
Round 1 - UQ  
24 hours  
Round 2 - UQ  
24 hours  
Round 3 - FQ  
2 hours  
Round 4 - UQ



d'Ettorre & Heinze 2005, *Current Biology*  
Dreier, van Zweden & d'Ettorre 2007, *Biology Letters*

...it is based on chemical cues

Discriminating between behavioral and chemical cues



In a Y maze, subordinate queens spent more time with the familiar than with the unfamiliar dominant queen  
(Wilcoxon test:  $Z = 3.0$ ,  $p = 0.035$ )



subordinate queen investigating an unfamiliar anesthetized dominant queen

In their own nest, subordinates investigated the unfamiliar queen longer as it represented an intruder  
(U-Test:  $U = 0.0$ ,  $p = 0.003$ )

Chemical cues are involved

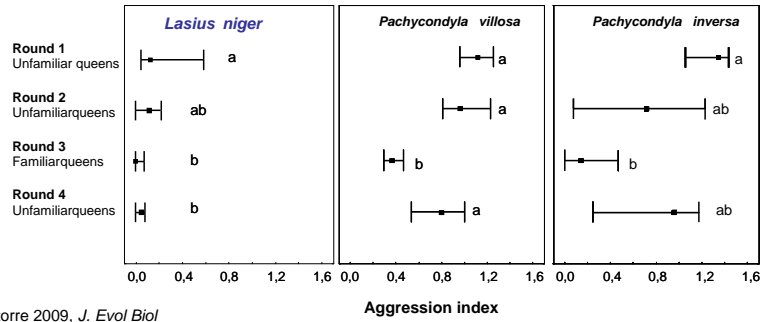
d'Ettorre & Heinze 2005, *Current Biology*



*Lasius niger*

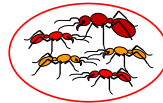
Co-founding queens do not form dominance hierarchies and only one queen survives when the workers appear

**Individual recognition does not occur**



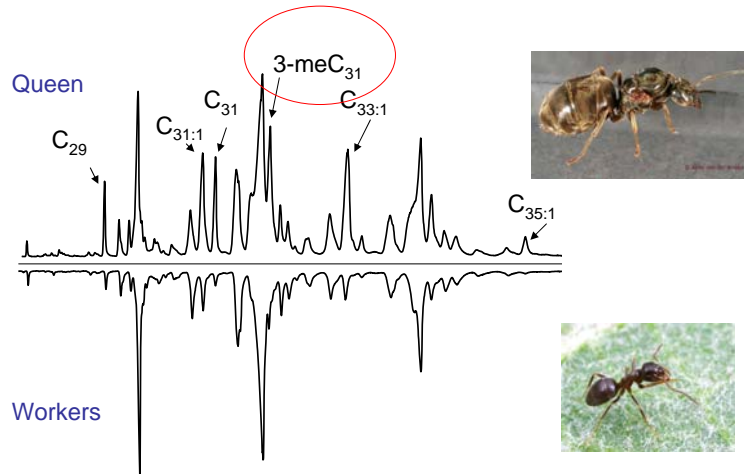
The variation in chemical recognition cues is comparable

intra-colony  
within-colony recognition



...in some cases a **single compound**  
can represent the identity signal

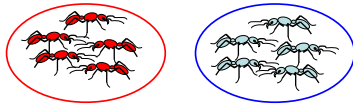
## Queen signal in *Lasius niger*



Luke Holman

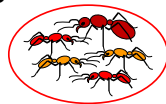
Synthesized by Charlotte Jørgensen

## Inter-colony level



*Formica rufibarbis*

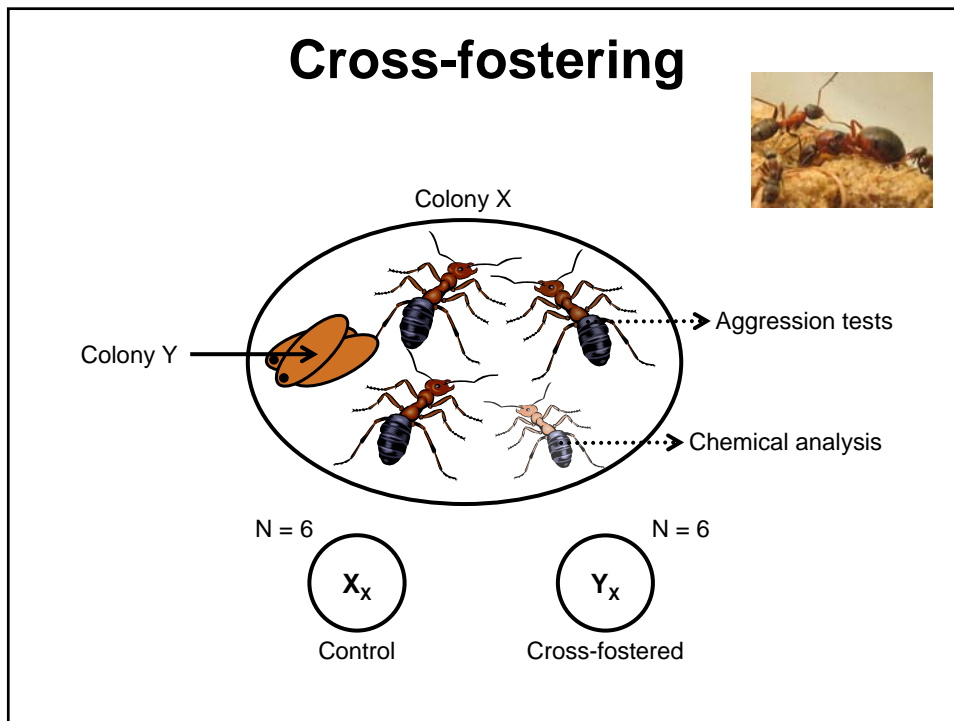
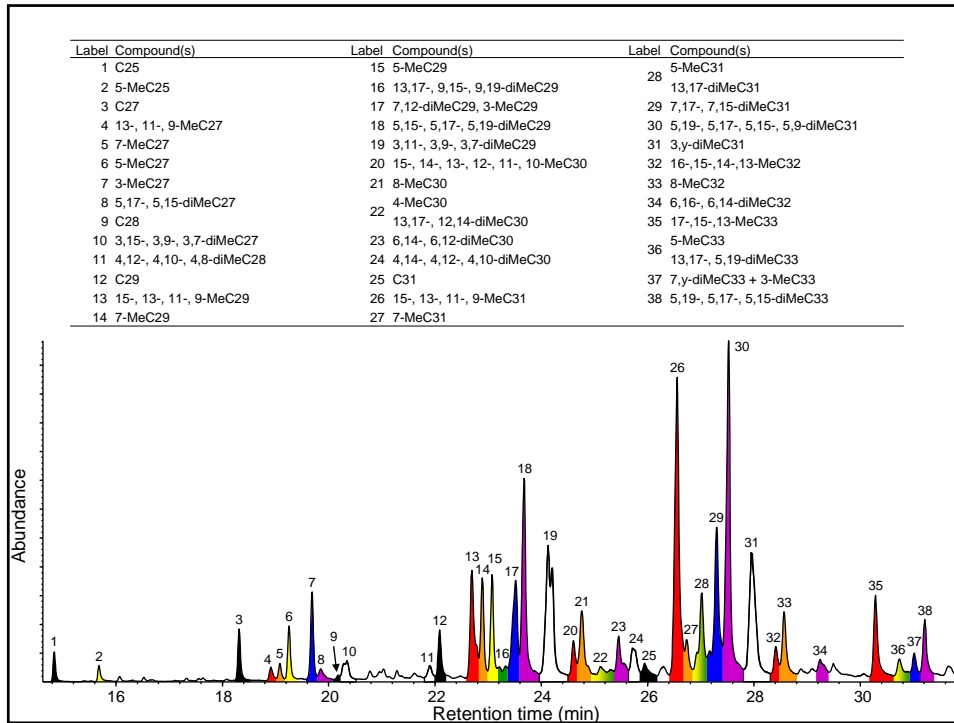
## Intra-colony

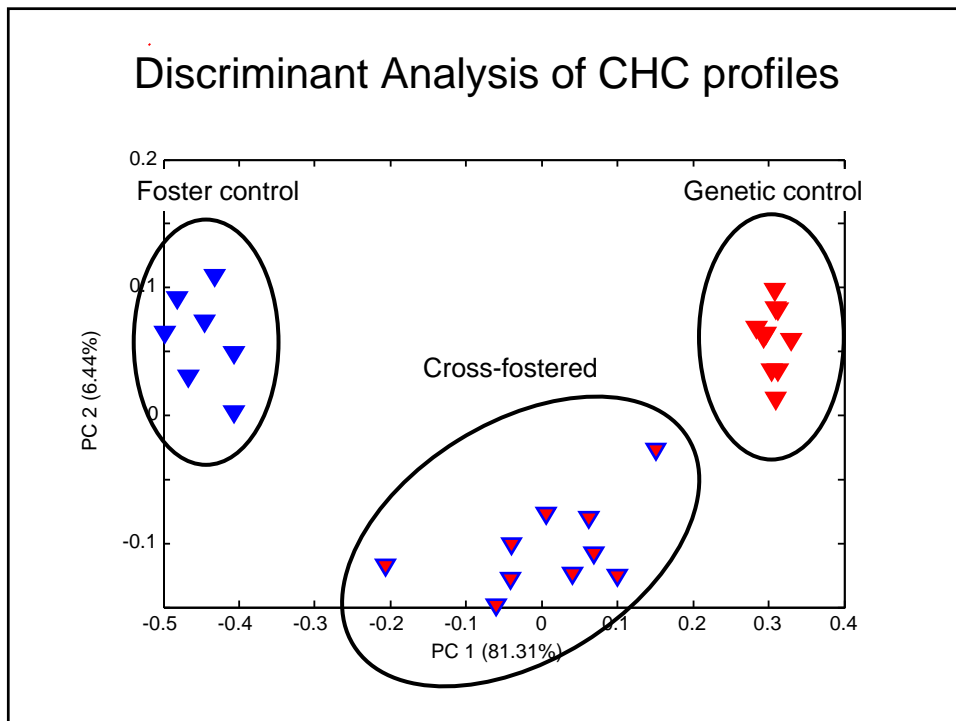
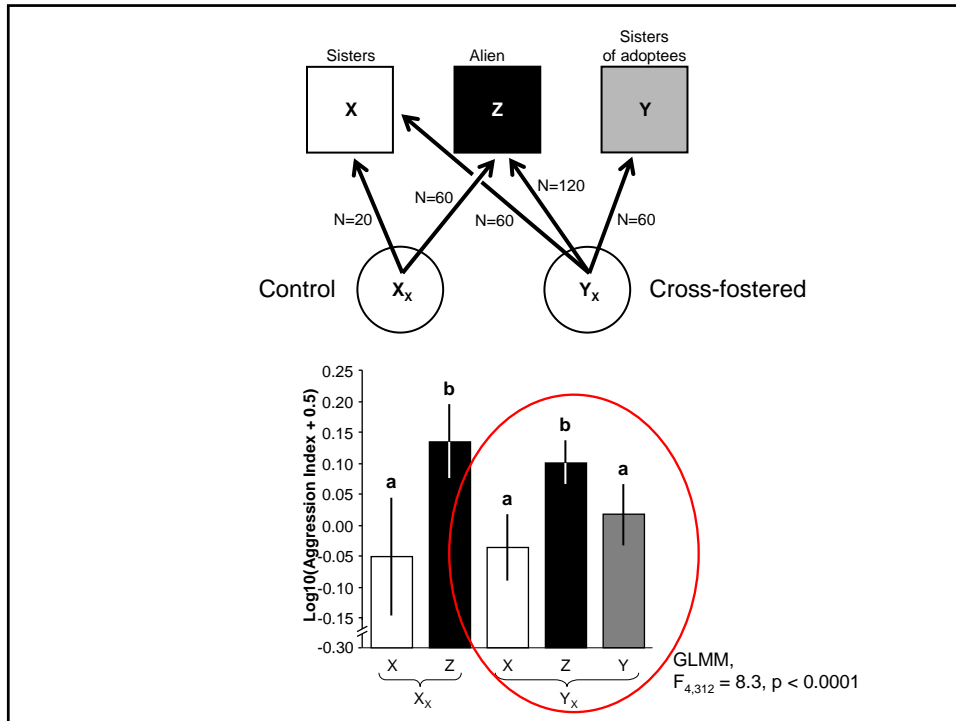


- Large colonies
- Monogynous
- Polyandrous (2-3 males)

Jelle van Zweden

Tim Linksvayer  
Jan H. Christensen





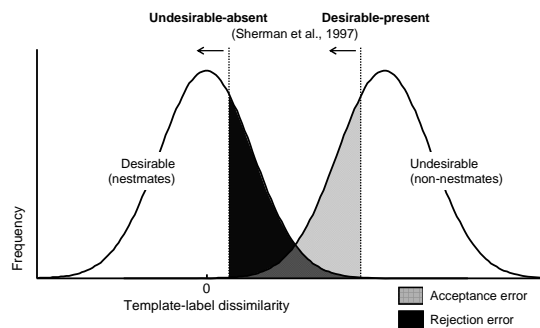
## Template-label matching

- Cuticular hydrocarbon profiles have a significant heritable component, but also an important environmental component
- Cuticular profiles may change over time
- Both label and template are not fixed

What kind of template can be both restrictive and flexible?



## Sherman *et al.* (1997) models based on phenotype matching



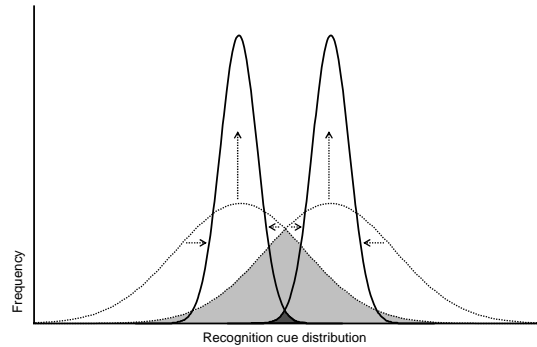
Arrows: the phenotypes that will be accepted under the respective model

**Desirable-present:** more **acceptance** errors

**Undesirable-absent:** more **rejection** errors



What happens if cues are mixed within each colony?

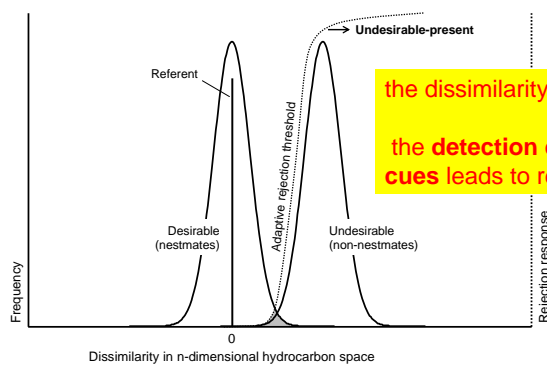


the distribution of recognition cues is narrowed

this reduces the probability of acceptance and rejection errors (shaded area)

What if ants recognize foes and not friends?

### The Gestalt non-nestmate recognition model (U-present)



Individuals are **habituated** (or desensitized) to the referent phenotype and will thus only detect dissimilarities from this phenotype

(shaded area = rejection errors)

Guerrieri et al 2009  
van Zweden & d'Ettorre, *in press*

Any data?

Nestmate recognition (between colonies)

Usually investigated with aggression tests

A new method allowing the separation of chemical  
and behavioural stimuli

Ant opening the mandibles



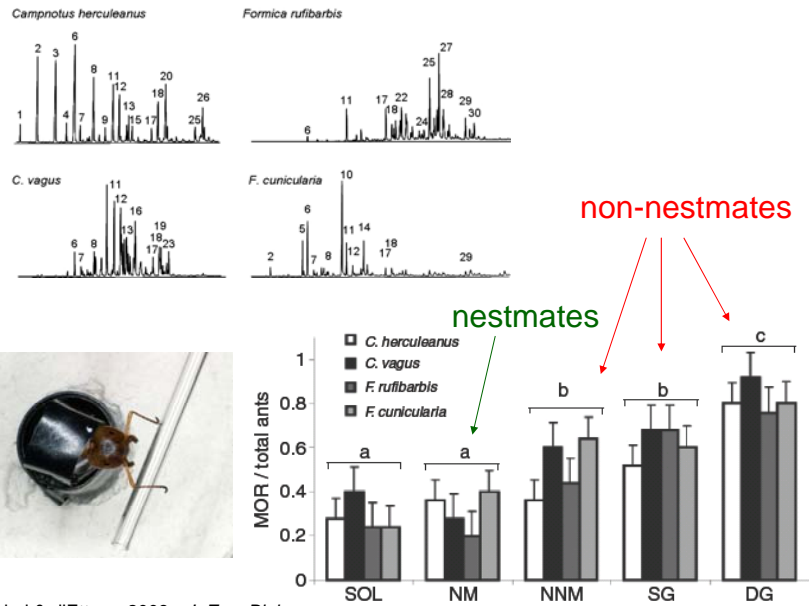
Ant not opening the mandibles



Fernando J. Guerrieri

Mandible opening response (MOR)

## Mandible opening response (MOR)

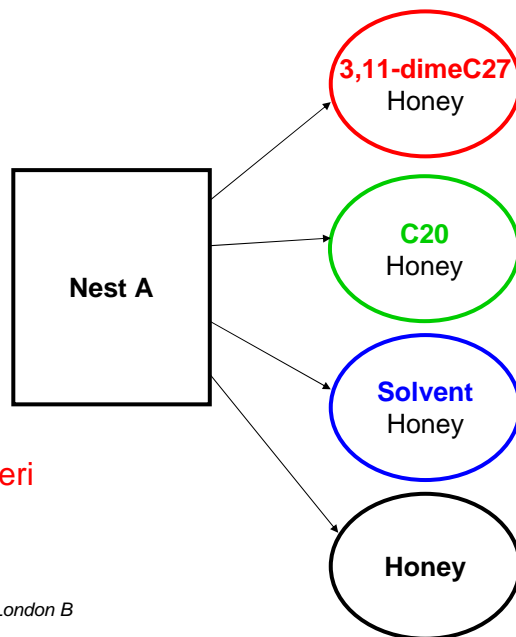


Guerrieri & d'Ettorre 2008 - *J. Exp. Biol.*



*Camponotus herculeanus*

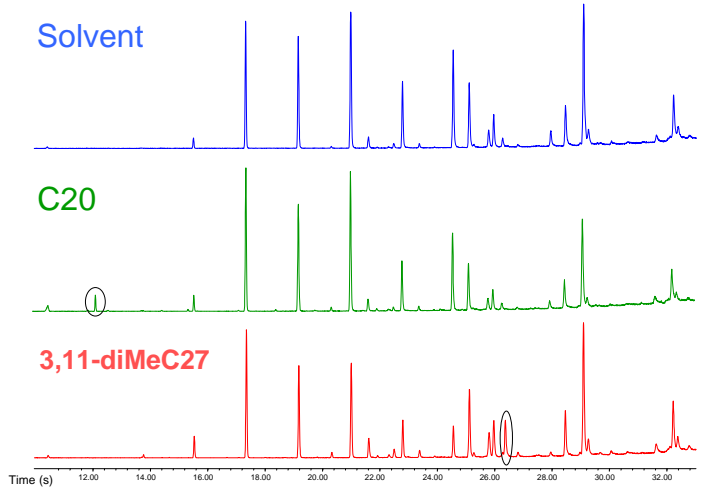
## Groups of workers



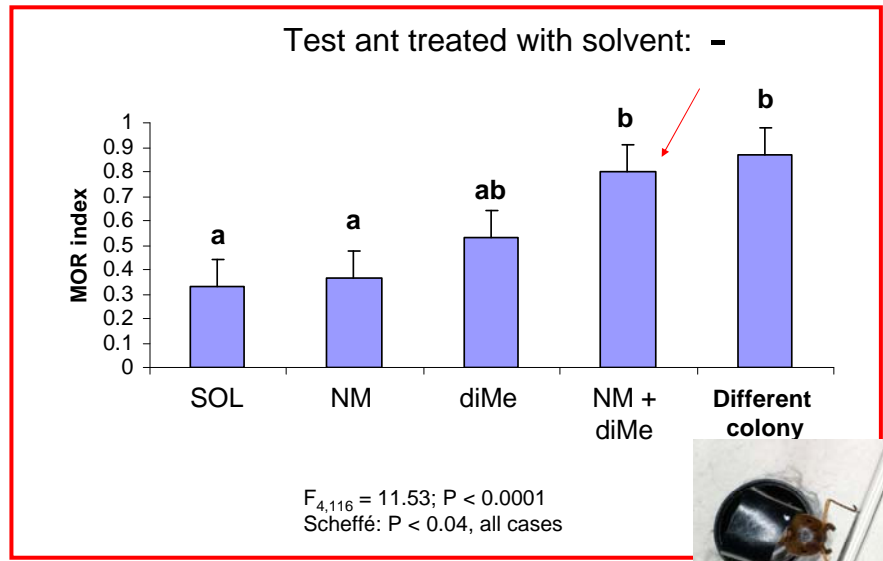
Fernando J. Guerrieri  
Volker Nehring  
Giovanni Galizia

Guerrieri et al 2009 *Proc R Soc London B*

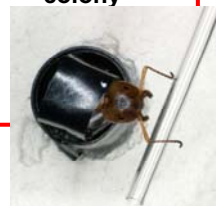
New hydrocarbon in the cuticular profile  
Solid Phase Micro Extraction (SPME)



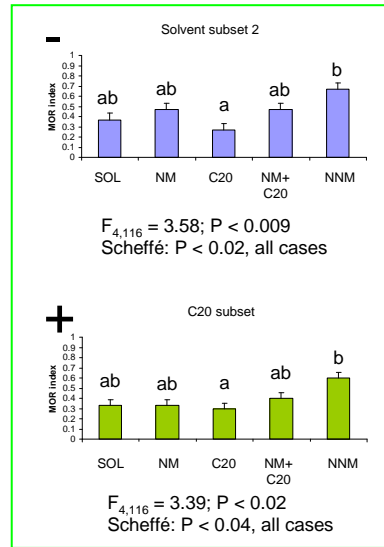
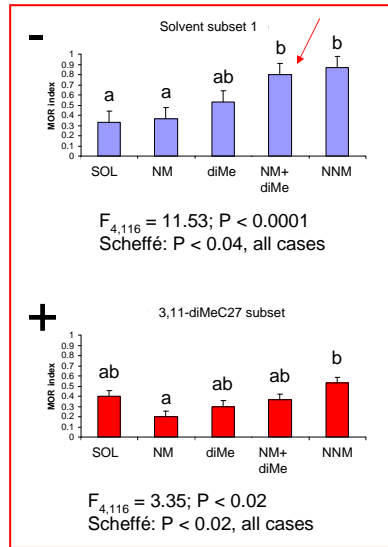
Mandible opening response of ants lacking the hydrocarbon



MOR index = MOR / total ants



## Mandible opening response



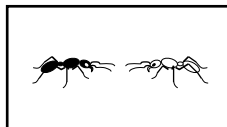
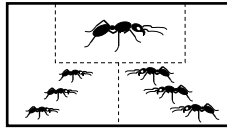
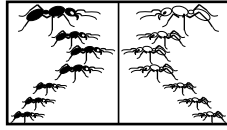
It is the **presence** –and not the absence- of a particular hydrocarbon on the cuticle that elicits aggression

Ants recognize foes and not friends!



...perhaps the bar-code model is wrong

## Future...



Can we predict adaptive processing pathways for each level of recognition?



Template

Label



Thank you!

