In the beginning there were chemicals

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MARIE CURIE ACTIONS

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"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

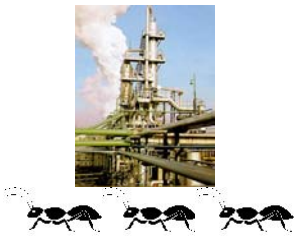
Commentary

Honest and dishonest communication in social Hymenoptera

J. Heinze[1,*] and P. d'Ettorre[2]

Modes of communication

- Acoustic
- Visual
- Tactile

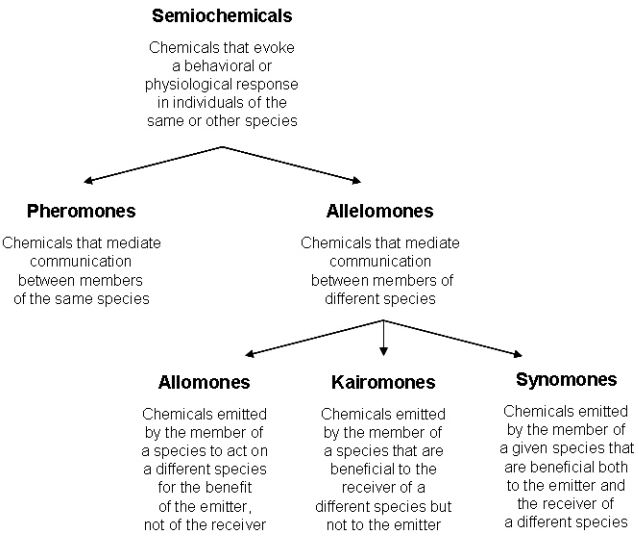


- **Chemical**

Semiochemical ⟶ substance used in communication

Pheromone (within species)

Allelomone (across species)



Sociobiology of Communication, Chapter 7 – G. de Brito Sanchez et al.

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**

Who is who?

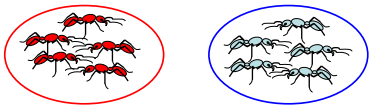
Group/society

Role

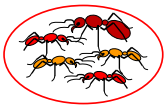
Individual

Communication of identity in ants
levels of recognition

inter-colony
nestmate recognition

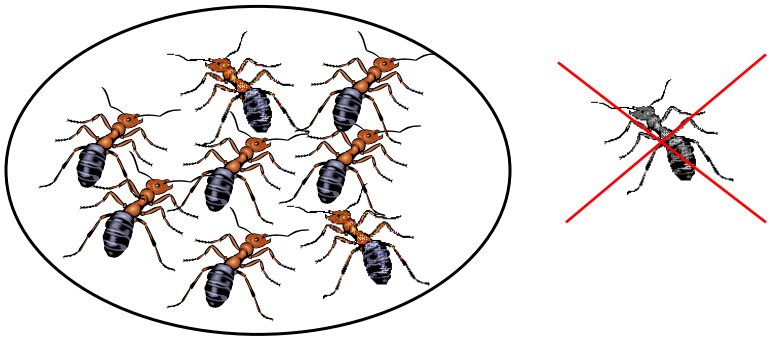


intra-colony
within-colony recognition



inter-individual
individual recognition

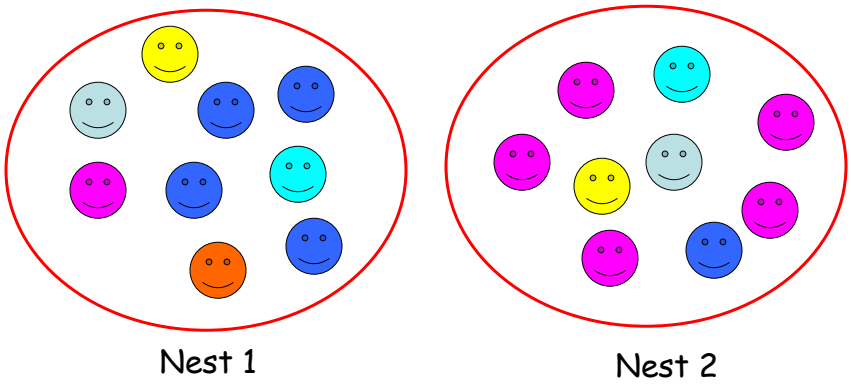
Insect societies are generally closed



Nestmate recognition is fundamental for social organisation

Nestmate recognition and Kin recognition are two different phenomena

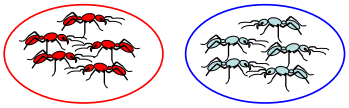
Mixed colonies



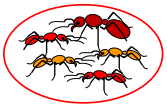
Same colour = kin

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



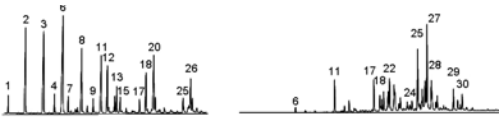
Kin recognition could take place **within** the colony, because the degrees of relatedness among nestmates can vary due to polyandry, polygyny or both.



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

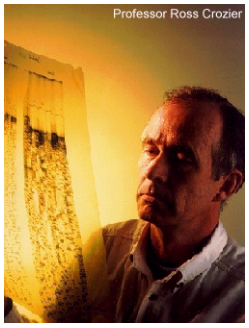
Individuals with **common** labels suffer low costs

↓

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

But recognition is possible!

The Crozier' paradox



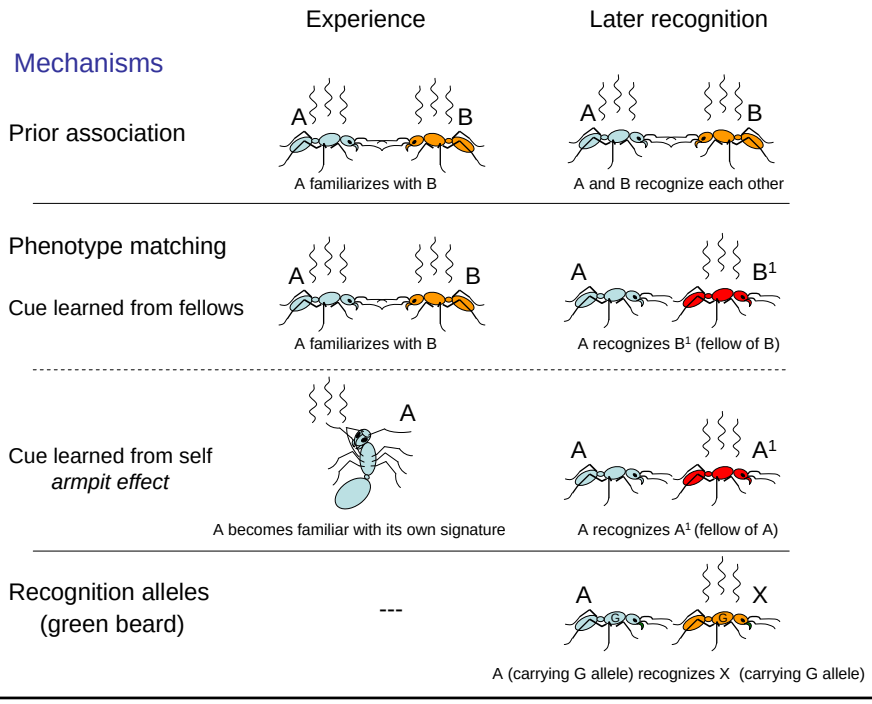
Crozier 1987

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

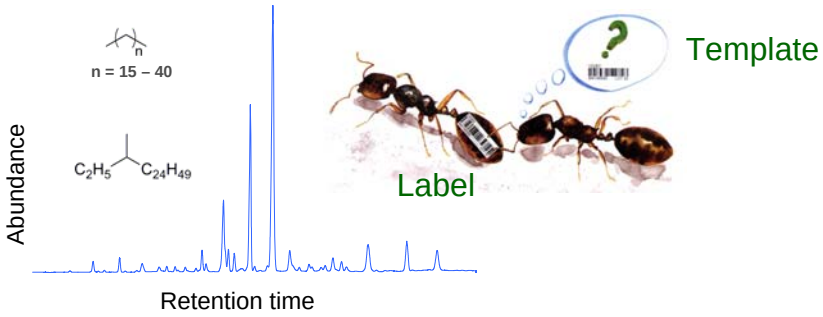
- Prior association
- Phenotype matching
- Recognition alleles (green beard)



Recognition cues

- In ants recognition cues are chemicals

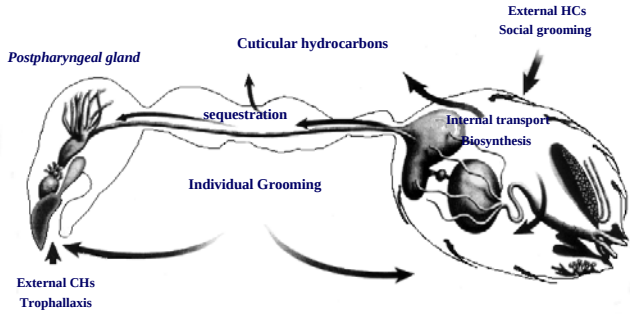
Cuticular hydrocarbons are considered to be the chemical cues responsible for recognition (label)



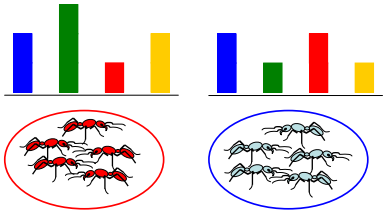
Nestmate recognition cues

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

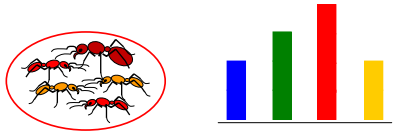
The colony odour is not the simple sum of cues of the different individuals, but it is a new configuration, a pattern of elements resulting into a unified whole (*Gestalt*)



Levels of recognition in ants

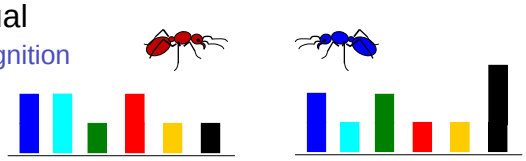


inter-colony
nestmate recognition



intra-colony
within-colony recognition

inter-individual
individual recognition



inter-individual
individual recognition

Pachycondyla villosa and *P. inversa*

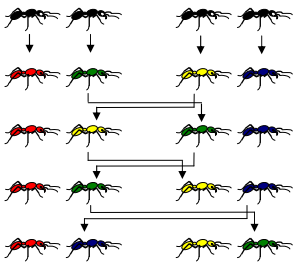
- Queens associate to found a new colony
- They establish a rank order regulating the division of labour

  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

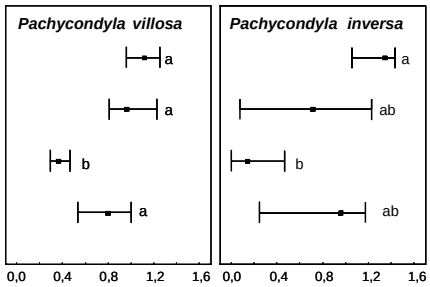


Round 1 - UQ
24 hours

Round 2 - UQ
24 hours

Round 3 - FQ
2 hours

Round 4 - UQ



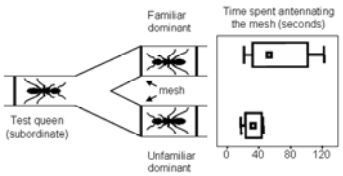
Aggression index

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)

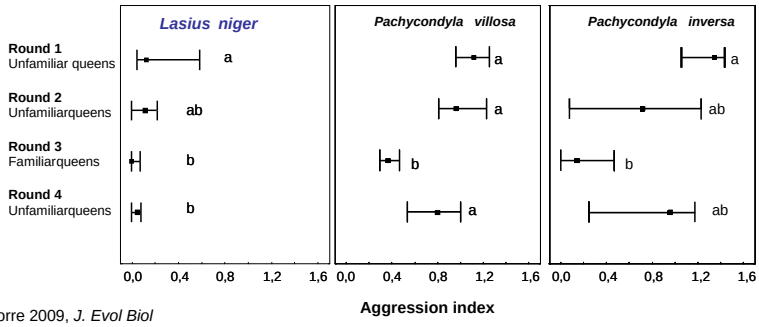
Chemical cues are involved

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

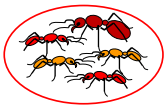
Individual recognition does not occur



Dreier & d'Ettorre 2009, *J. Evol Biol*

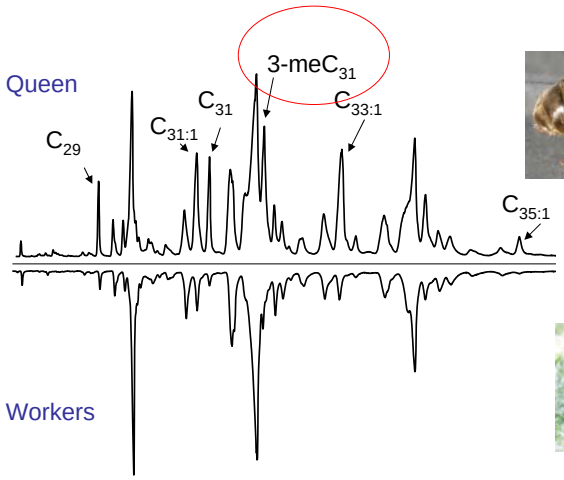
The variation in chemical recognition cues is comparable

intra-colony
within-colony recognition



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

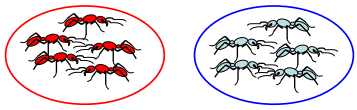
Queen signal in *Lasius niger*



Luke Holman

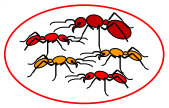
Synthesized by Charlotte Jørgensen

Inter-colony level



Formica rufibarbis

Intra-colony

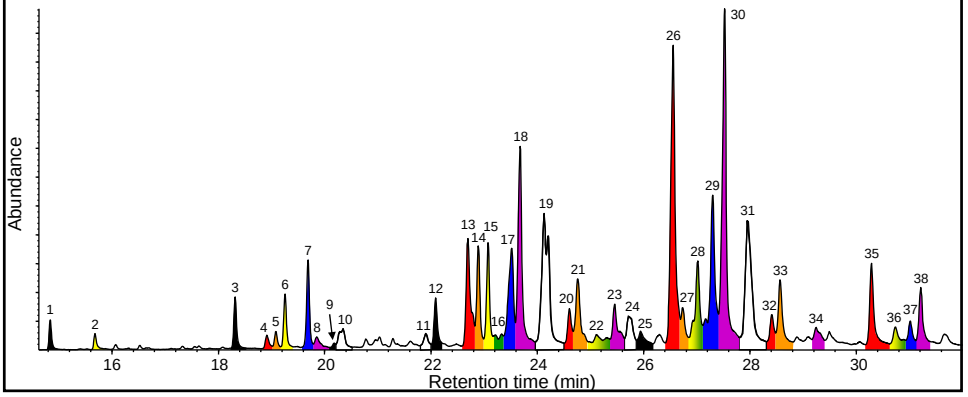


- Large colonies
- Monogynous
- Polyandrous (2-3 males)

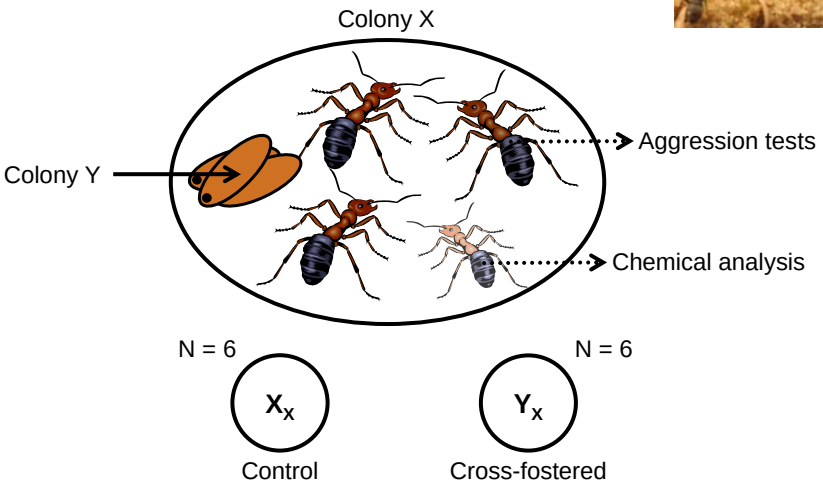
Jelle van Zweden

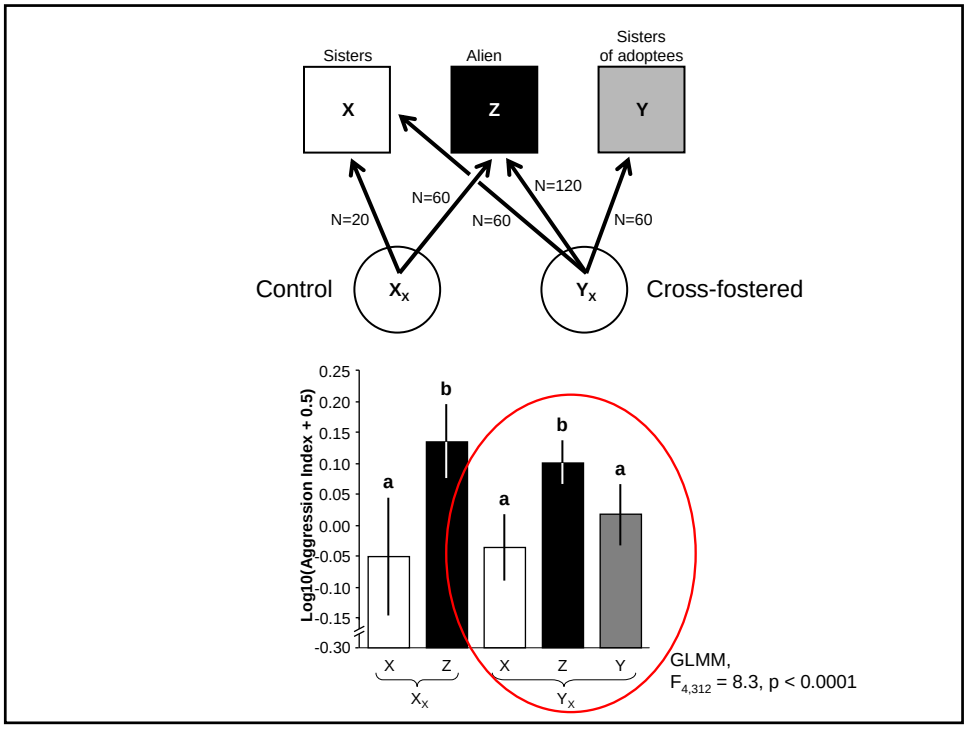
Tim Linksvayer
Jan H. Christensen

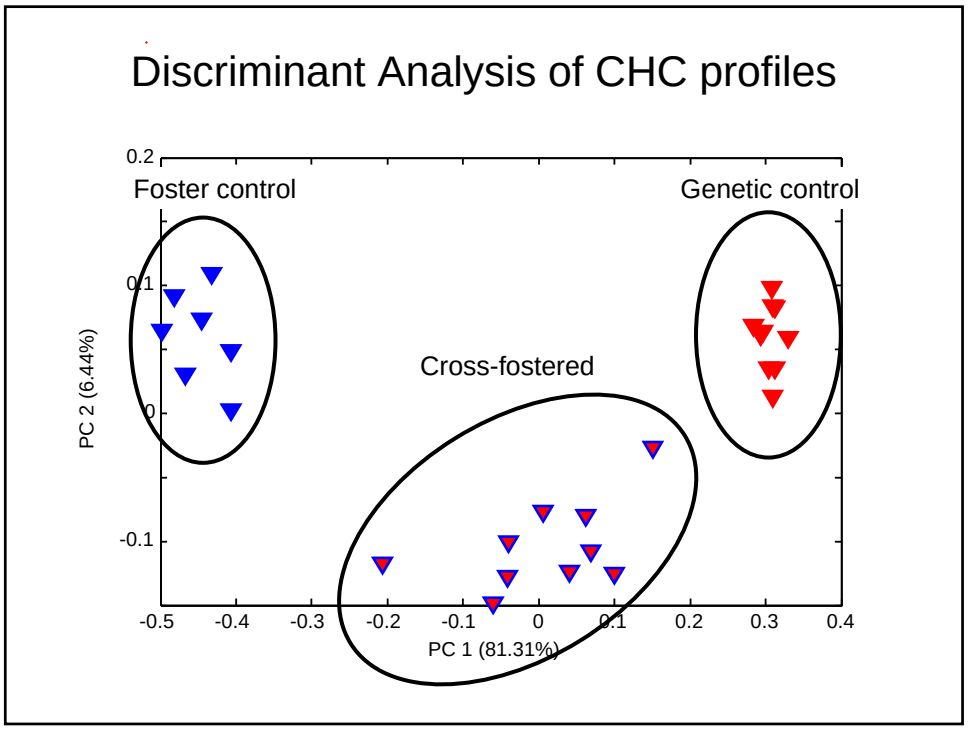
Label	Compound(s)	Label	Compound(s)	Label	Compound(s)
1	C25	15	5-MeC29	28	5-MeC31
2	5-MeC25	16	13,17-, 9,15-, 9,19-diMeC29		13,17-diMeC31
3	C27	17	7,12-diMeC29, 3-MeC29	29	7,17-, 7,15-diMeC31
4	13-, 11-, 9-MeC27	18	5,15-, 5,17-, 5,19-diMeC29	30	5,19-, 5,17-, 5,15-, 5,9-diMeC31
5	7-MeC27	19	3,11-, 3,9-, 3,7-diMeC29	31	3,y-diMeC31
6	5-MeC27	20	15-, 14-, 13-, 12-, 11-, 10-MeC30	32	16-,15-,14-,13-MeC32
7	3-MeC27	21	8-MeC30	33	8-MeC32
8	5,17-, 5,15-diMeC27	22	4-MeC30	34	6,16-, 6,14-diMeC32
9	C28		13,17-, 12,14-diMeC30	35	17-,15-,13-MeC33
10	3,15-, 3,9-, 3,7-diMeC27	23	6,14-, 6,12-diMeC30	36	5-MeC33
11	4,12-, 4,10-, 4,8-diMeC28	24	4,14-, 4,12-, 4,10-diMeC30		13,17-, 5,19-diMeC33
12	C29	25	C31	37	7,y-diMeC33 + 3-MeC33
13	15-, 13-, 11-, 9-MeC29	26	15-, 13-, 11-, 9-MeC31	38	5,19-, 5,17-, 5,15-diMeC33
14	7-MeC29	27	7-MeC31		



Cross-fostering




Sisters
Alien
Sisters of adoptees
X
Z
Y
N=20
N=60
N=60
N=120
N=60
Control
X_X
Y_X
Cross-fostered
Log10(Aggression Index + 0.5)
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.30
a
b
a
b
a
X
Z
X
Z
Y
X_X
Y_X
GLMM,
$F_{4,312}$ = 8.3, p < 0.0001

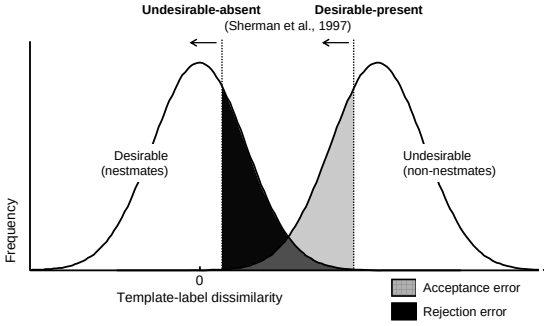

Discriminant Analysis of CHC profiles
Foster control
Genetic control
Cross-fostered
PC 2 (6.44%)
PC 1 (81.31%)
0.2
0.1
0
-0.1
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4

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

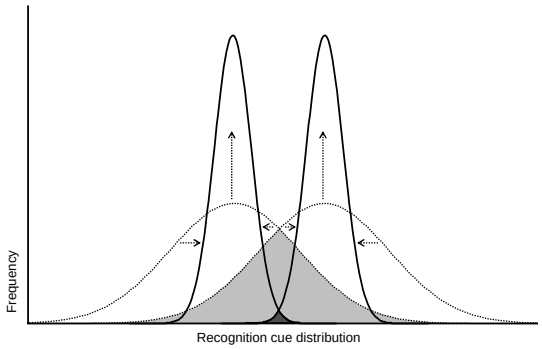


Arrows: the phenotypes that will be accepted under the respective model

Desirable-present: more acceptance errors

Undesirable-absent: more rejection errors

What happens if cues are mixed within each colony?



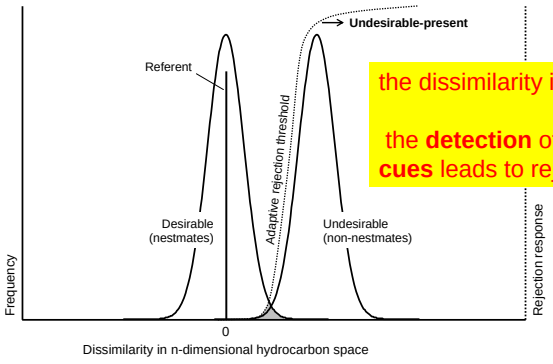
the distribution of recognition cues is narrowed

↓

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)



the dissimilarity is large enough:

the **detection** of **undesirable cues** leads to rejection

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

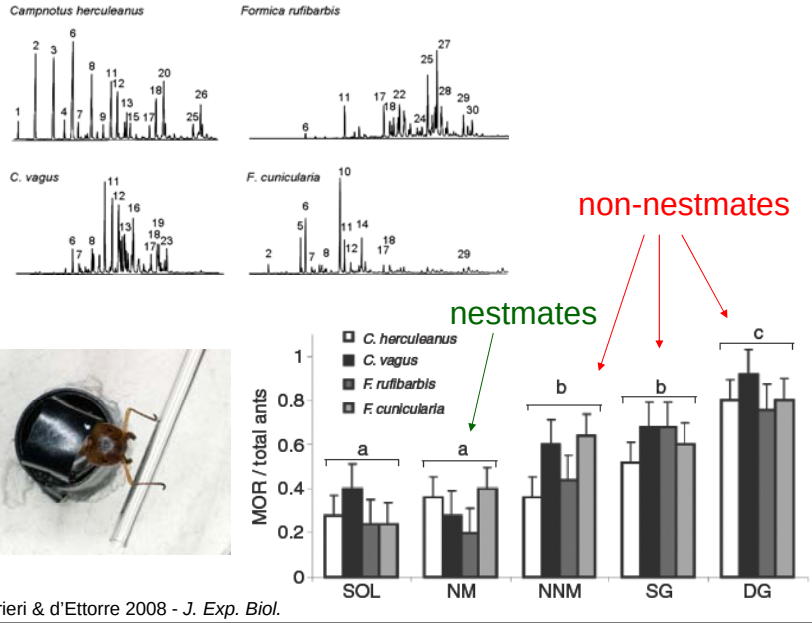
Ant opening the mandibles

Ant not opening the mandibles

Fernando J. Guerrieri

Mandible opening response (MOR)

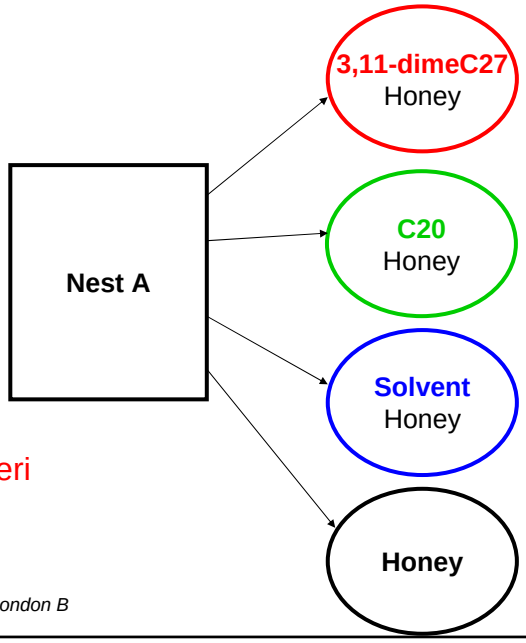
Mandible opening response (MOR)



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

Groups of workers

Camponotus herculeanus

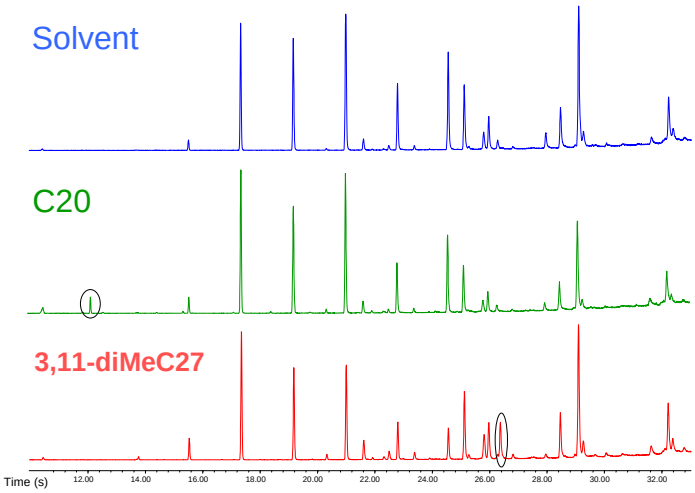


Fernando J. Guerrieri
Volker Nehring
Giovanni Galizia

Guerrieri et al 2009 *Proc R Soc London B*

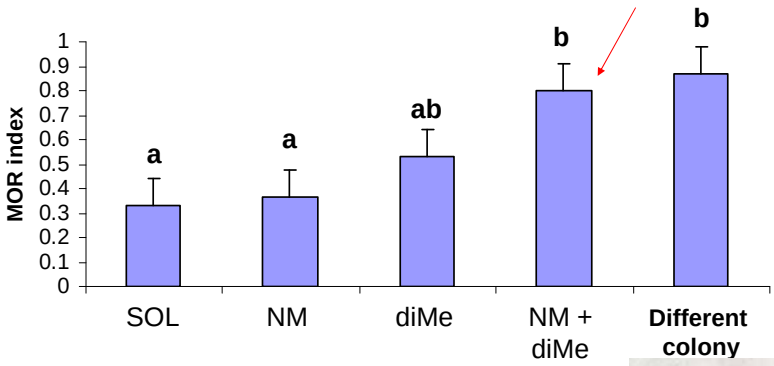
New hydrocarbon in the cuticular profile

Solid Phase Micro Extraction (SPME)



Mandible opening response of ants lacking the hydrocarbon

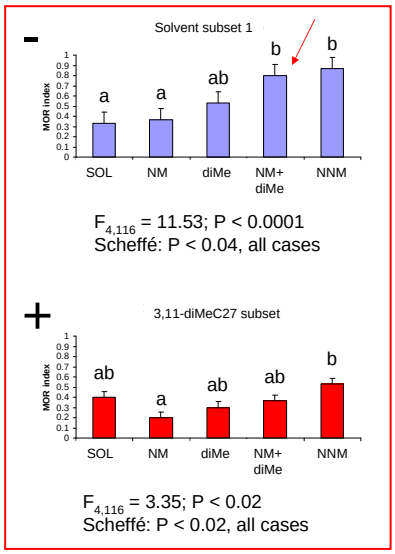
Test ant treated with solvent: –



$F_{4,116} = 11.53$; $P < 0.0001$
Scheffé: $P < 0.04$, all cases

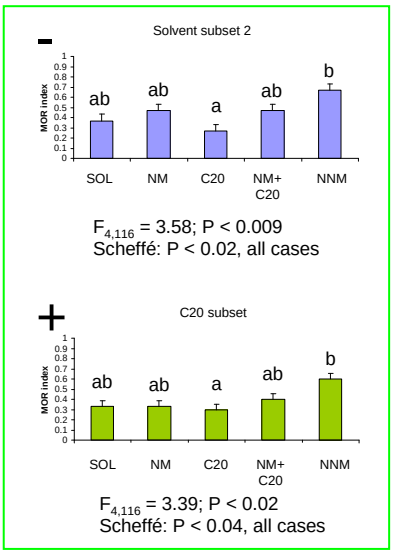
MOR index = MOR / total ants

Mandible opening response



$F_{4,116} = 11.53$; $P < 0.0001$
Scheffé: $P < 0.04$, all cases

$F_{4,116} = 3.35$; $P < 0.02$
Scheffé: $P < 0.02$, all cases



$F_{4,116} = 3.58$; $P < 0.009$
Scheffé: $P < 0.02$, all cases

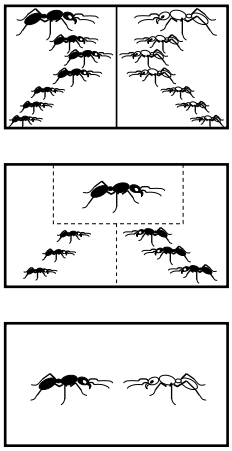
$F_{4,116} = 3.39$; $P < 0.02$
Scheffé: $P < 0.04$, all cases

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?

MARIE CURIE ACTIONS

Thank you!

Centre for Social Evolution