Role of information for mate acquisition and sex ratio manipulation in the parasitic wasp *Venturia canescens*

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- During their lifetime, animals often have to choose between several options.
- The decision making processes, and the behaviors that result from them, influence chances of survival and of successful reproduction.
- Under variable environmental conditions, the acquisition of information is essential, because it reduces future uncertainty and thus improves the probability of success.

INFORMATION ?

Chemical (olfactory or gustative), visual, tactile, auditory…

INFORMATION ?

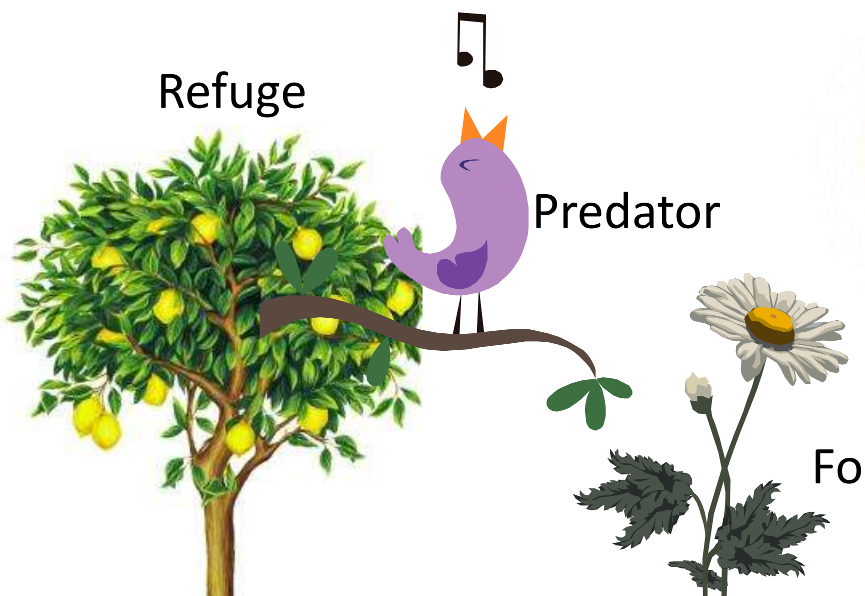
Environment

Abiotic conditions

Biotic conditions

Habitat

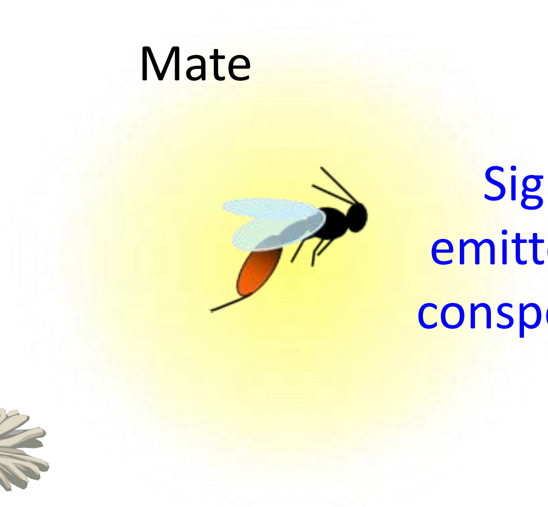
Refuge



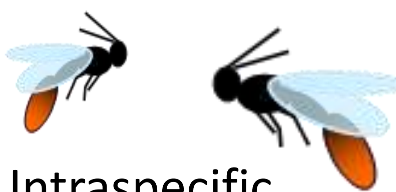
Predator

Food resource

Mate



Signal emitted by conspecifics

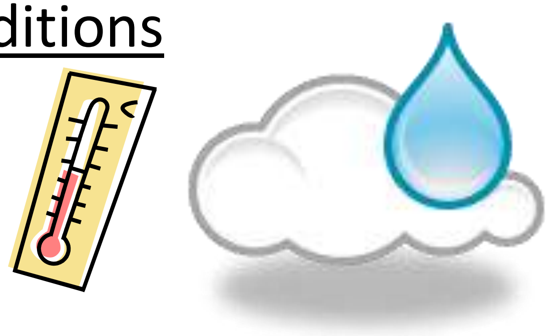


Intraspecific competitors

INFORMATION ?

Environment

Abiotic conditions



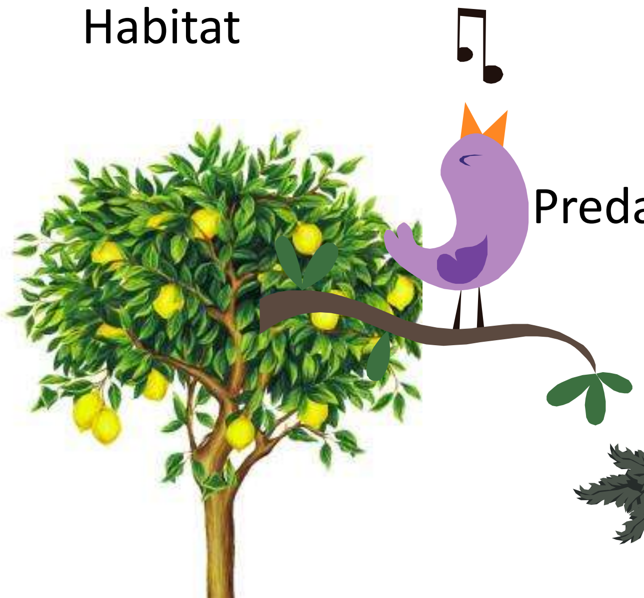
Biotic conditions

Internal state

Age,
mating status,
nutritional reserves…

Mate

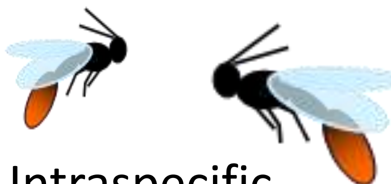
Habitat



Predator

Food resource

Signal emitted by conspecifics



Intraspecific competitors

- Decision makings that occur during the mating sequence

Σ of reproductive interactions between males and females

✓ When and where find/attract a mating partner ?

✓ How to choose it/be chosen by it?

✓ How many partners to have ?

✓ Should the male stay to help or go ?

First step of mating sequence = mate location strategies :

Search randomly in the environment << Use relevant information

→ increases encounter probability

- Main selective force acting on mating sequence : SEXUAL SELECTION

Differential reproduction owing to variation in the ability to obtain mates

Anisogamy
Number of ♂ gametes >> ♀ gametes

↓

Competition between ♂ gametes for the access of ♀ gametes

↓

Intensity of Sexual selection ♂ > ♀

Parental Investment of female > male

Competition between males for access to females

Mate choice by females

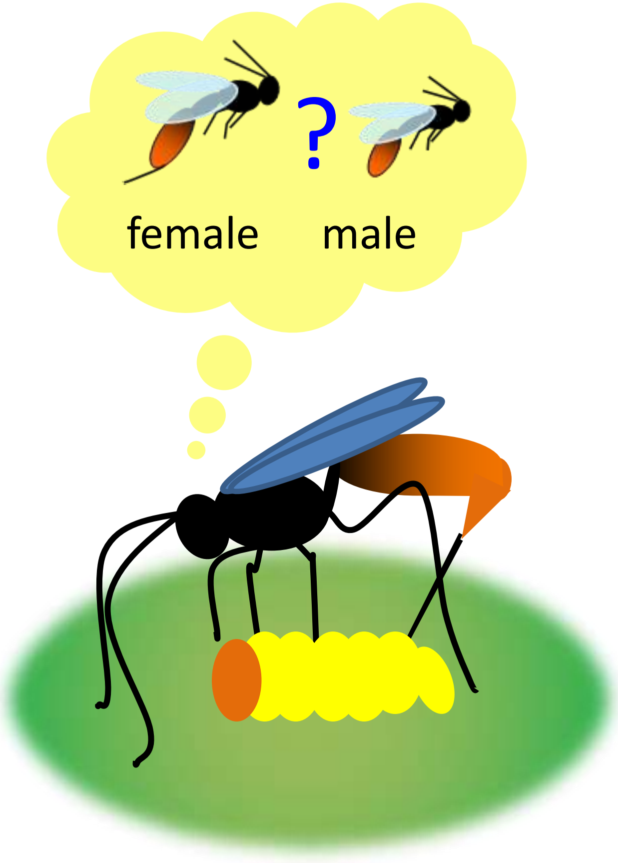
- Decision making occurring after the mating sequence

SEX ALLOCATION THEORY

✓ Proportion of male offspring or sex ratio is a trait submitted to selection

✓ Decision that depends on the previous steps (mating sequence): theoretical models of sex ratio evolution predict that optimal SR depends on the mating system through intensity of sexual selection (Hamilton 1967, Trivers et Willard 1973)

✓ Numerous evidences of organisms that manipulate their sex ratio in response to environmental variations and internal factors



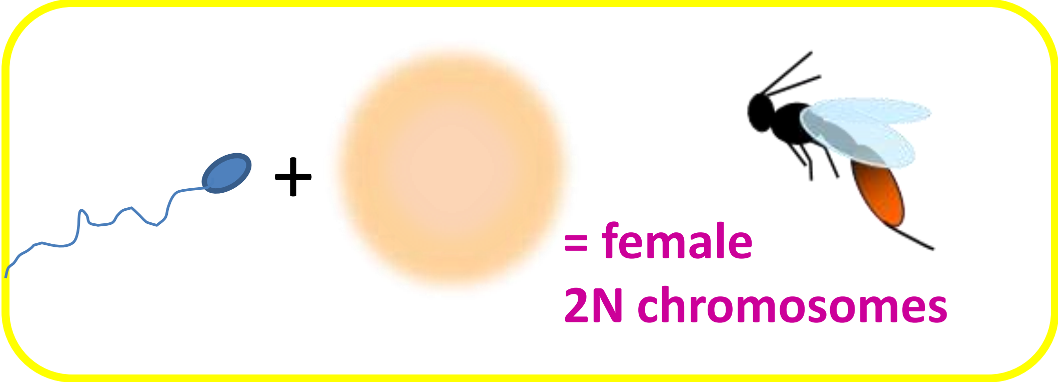
- Biological model : parasitic wasps

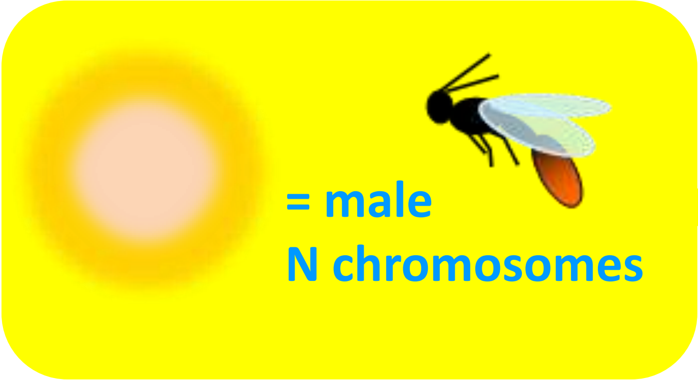
Parasitoids are insects that have a free-living adult stage but with larva having a parasitic live-style (develops inside or on another arthropod). Parasitic larva kill their host as a consequence of their development.

- Sex determination system in hymenoptera (1/2)

HAPLODIPLOID

Egg fertilization determines sex of the offspring



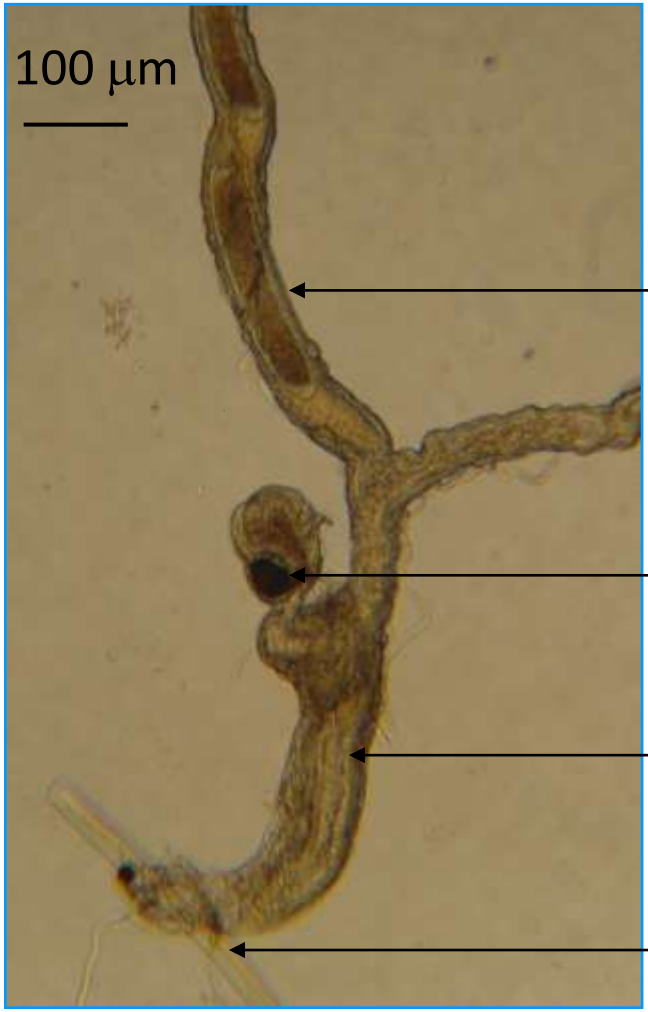


Virgin females can reproduce but only have sons

- Sex determination system in hymenoptera (2/2)

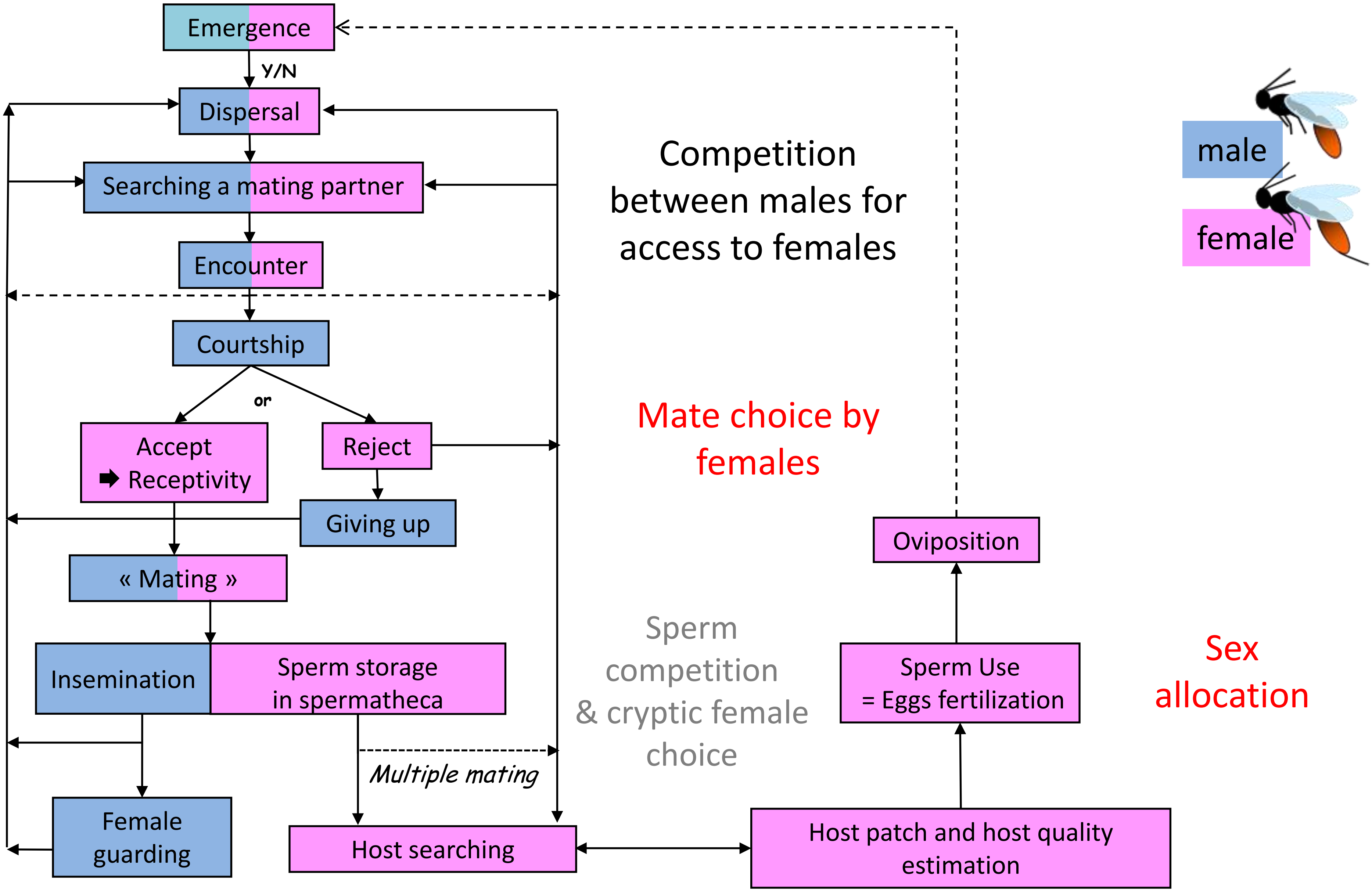
Opening/closing of the spermatheca

Sex ratio manipulation



Venturia canescens. Picture: C. Bressac

- Mating sequence in parasitoid : chronology of events and decision making



General objective of the thesis

- To determine the role of the various information involved in the decision making processes during
  - Mate acquisition : mate finding & mate choice
  - Sex allocation

- Biological model : parasitic wasps

- Information related directly and indirectly to conspecifics

- Combination of information

Venturia canescens Gravenhorst

- Solitary parasitoid of Pyralid larvae
- Model species in ecology since 1930
- Sexual reproduction mode at the end of 90's (Beukeboom et al 1999)

Sex ratio < 0.5 ?

↕

Mating system ???

= Σ mate location strategies, number of mate, choice criterion

…

Part 1 : Which strategies are used by males and females in mate searching ?

Part 2 : Is avoidance of sibmating a criterion of mate choice ?

Part 3 : Does constrained oviposition influence offspring sex ratio in the solitary parasitoid wasp *Venturia canescens ?*

Metzger, M., Bernstein, C., & Desouhant, E. (2008)

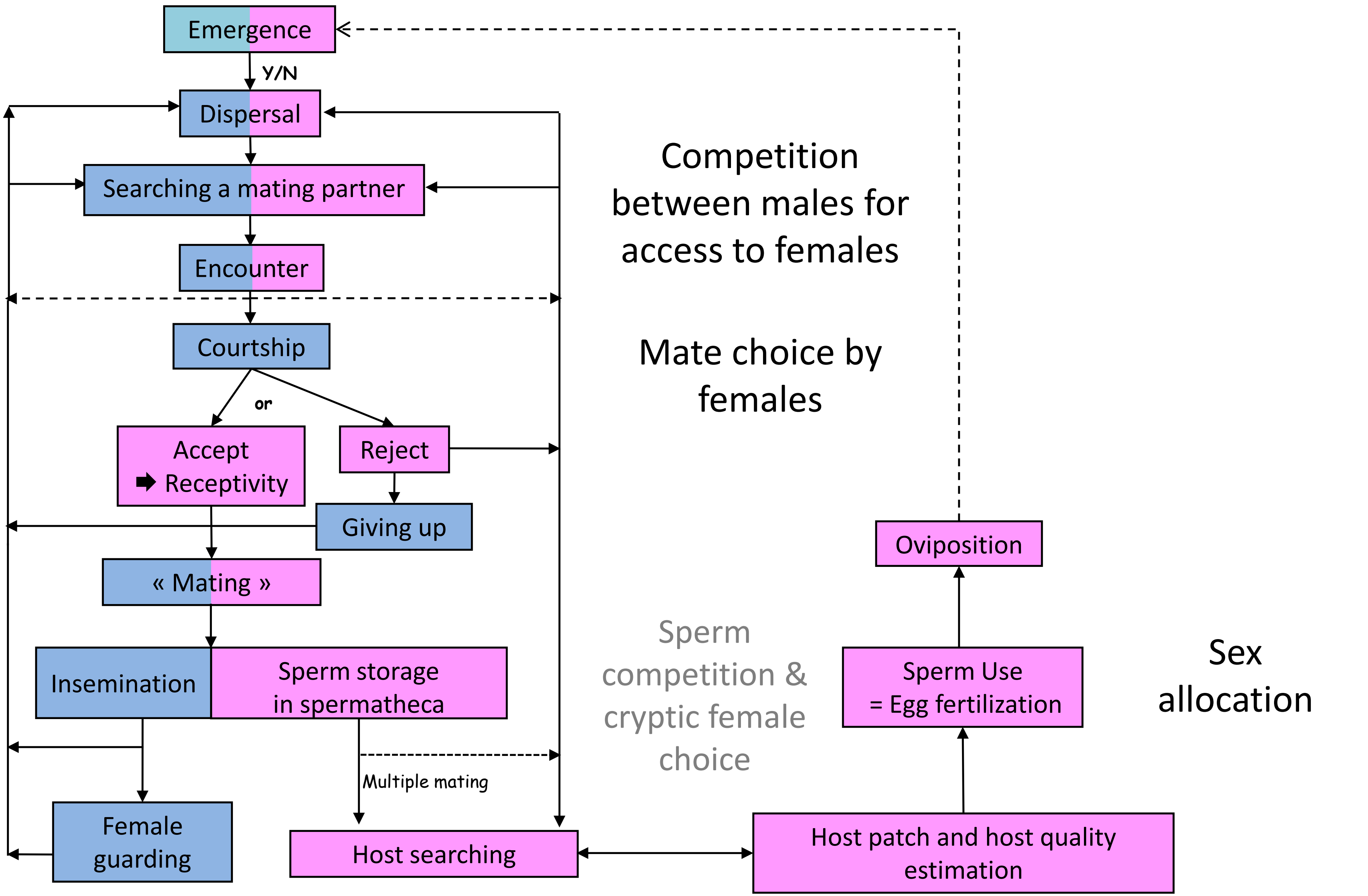
Ecological Entomology, ***33, 167-174.***

Part I

Mate finding in a parasitic wasp is mediated by several cues

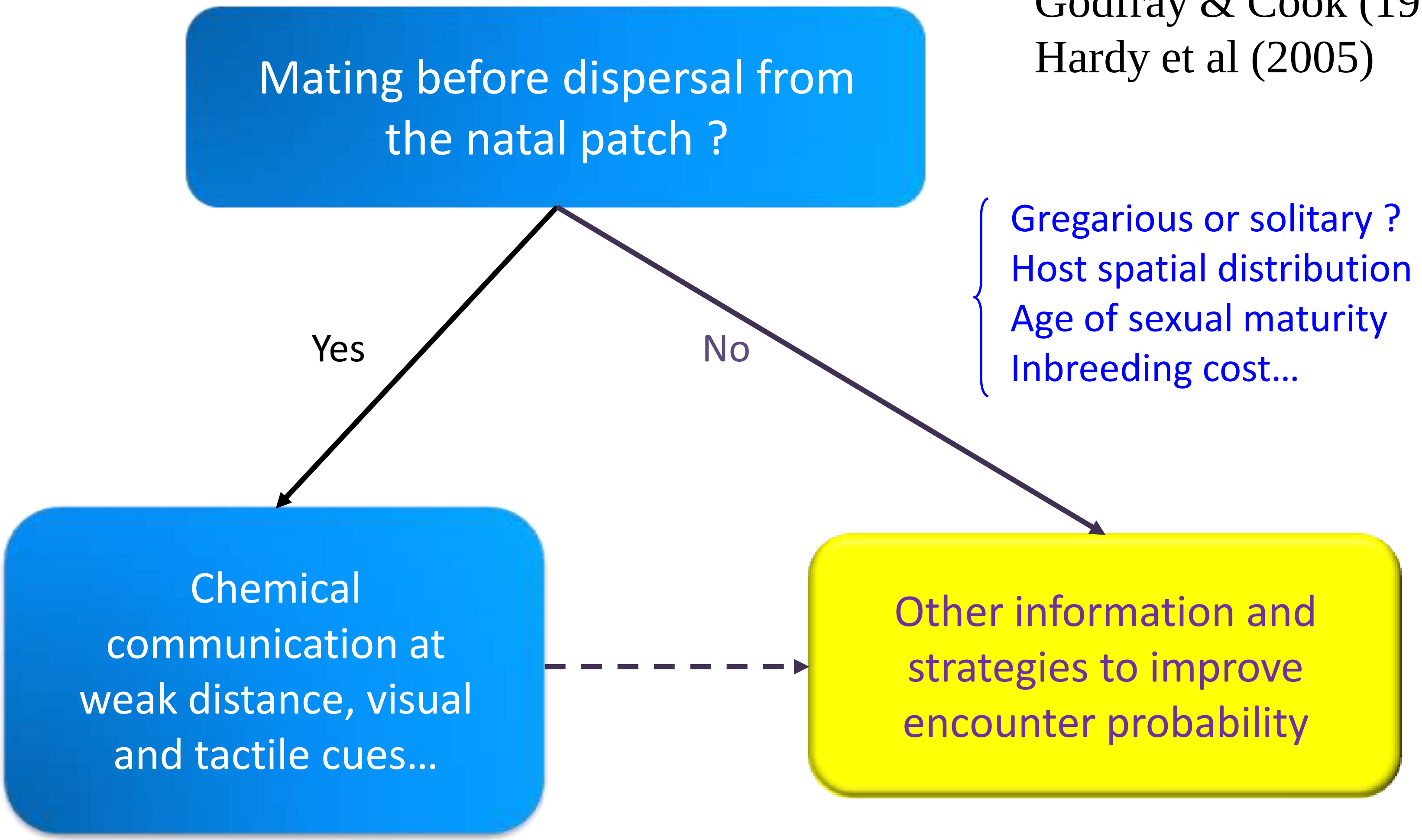
Metzger M., Fischbein D., Auguste A , Fauvergue X., Bernstein C. & E. Desouhant, *In prep.*

- Mating sequence in parasitoid : chronology of events and decision making



- Parasitoid mating system & mate location

Godfray & Cook (1997)
Hardy et al (2005)



Usual in gregarious and quasi gregarious

Necessary for true solitary

- When matings occur after dispersal from the natal patch, how to locate a mate ?

1. With the help of the other sex (using intraspecific signalling)

Parasitoid : ♀ signal & ♂ search

Volatile sex pheromone (Kainoh 1999)

Trail pheromone left on the substrate (Fauvergue et al 1995)

- When matings occur after dispersal from the natal patch, how to locate mate ?

1. With the help of the other sex (using intraspecific signaling)

2. Searching mate in places where they should be (using environmental cues)

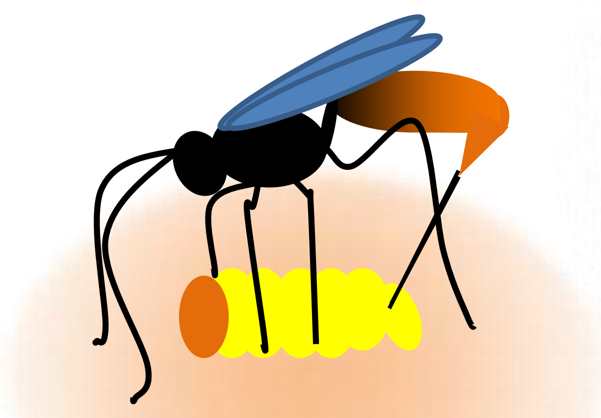
Host Kairomones

Volatile emitted by plants

…

Food

Natal patch
or oviposition site



- When matings occur after dispersal from the natal patch, how to locate mate ?

1. With the help of the other sex (using intraspecific signaling)
2. Searching partner in places where they should be (using environmental cues)
3. Mating swarm

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1. With the help of the other sex (using intraspecific signaling)
2. Searching partner in places where they should be (using environmental cues)
3. Mating swarm

Mixed mating system ?

Using several information's sources
should improve mate searching efficiency

Venturia canescens caracteristics

- Solitary parasitoid
- Non aggregative spatial distribution
- Low rate of parasitism

} In the field (Driessen & Bernstein 1999, Schneider 2003)

⇨ Males and females should frequently emerge from separated places and find a mate could be difficult.

- Females use kairomones to locate hosts (Corbet, 1971)

⇨ Males may use the same olfactory information than females to locate oviposition or emergence sites

- Females are able to integrate several information sources in decision making process when they forage for hosts (Castelo et al 2003, Lucchetta et al 2007)

Aim of this study

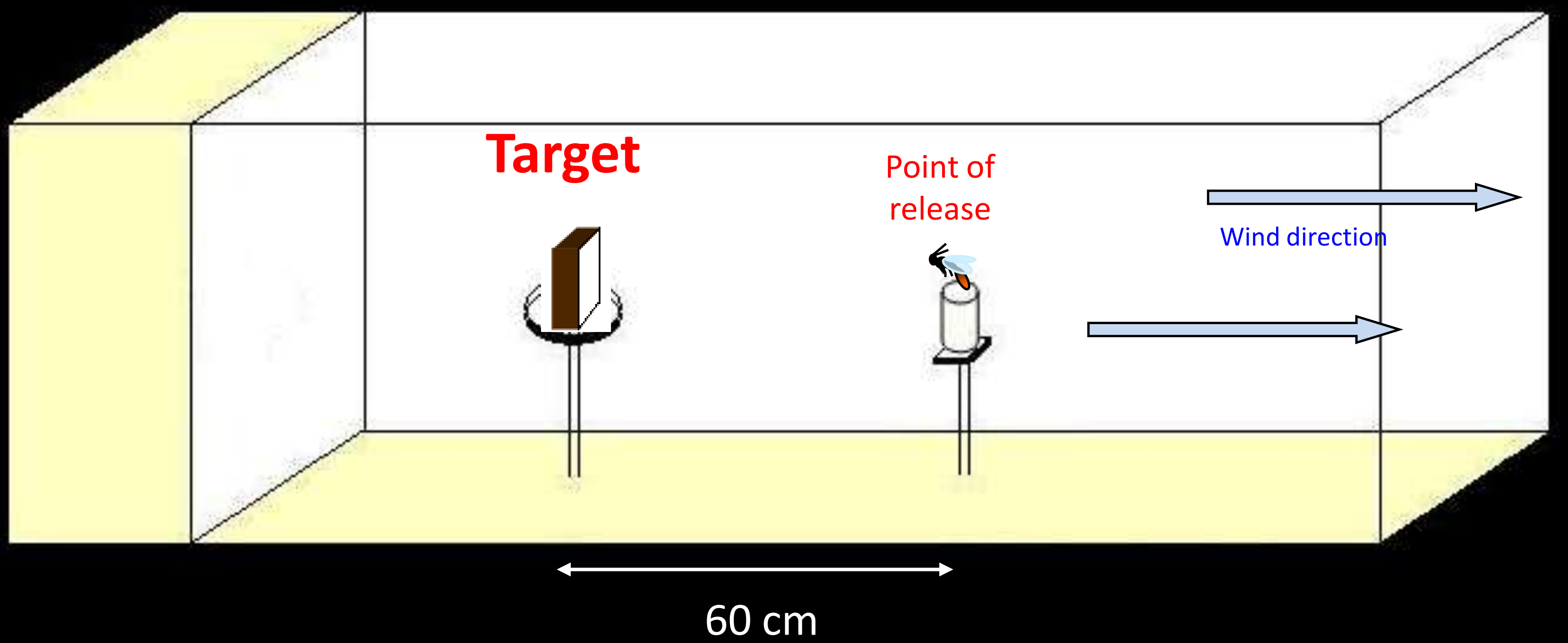
Which olfactory information are used to search a mate from a distance in the solitary parasitoid *Venturia canescens* ?

How information is used?

<u>First experiment testing whether :</u>

- Males are attracted by females and/or vice versa
- Hosts are attractives for males
- Association of hosts and conspecifics odours influence or not the mate location efficiency

INRA Sophia-Antipolis – collaboration X. Fauvergue



Collected data

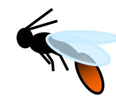
- Time before taking off
- Whether the target was reached or not

Part I. Mate finding : Experience 1 – Material and method

Experimental plan with 3 factors :

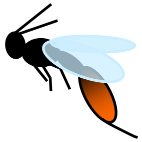
- Sex of the olfactory information receiver

male



ou

female



Aged of 1 day

Virgin

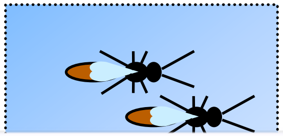
Feed

Target

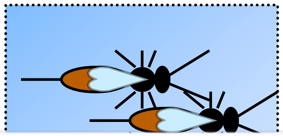
- Sex of emitter

No wasp

or



or



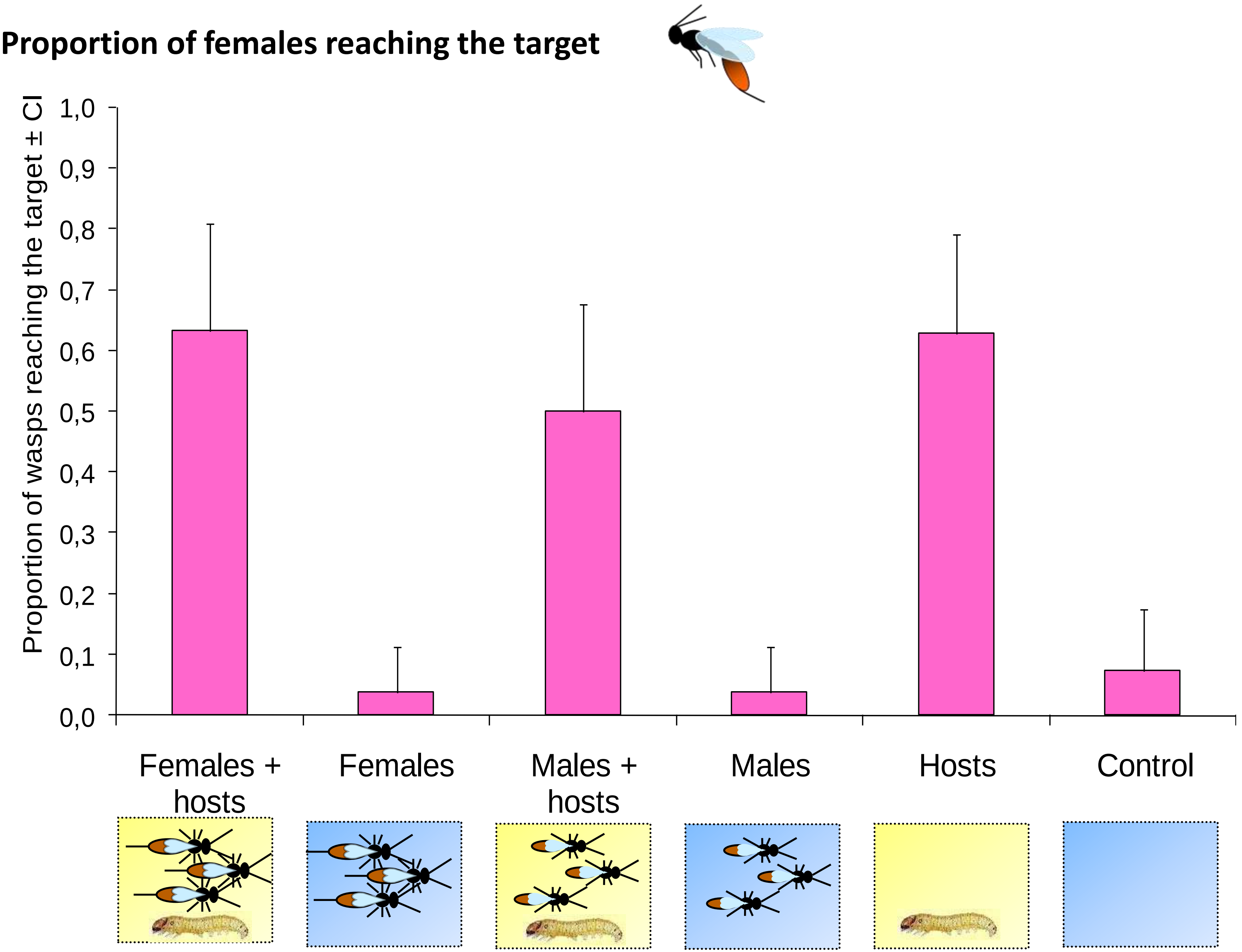
- Host presence

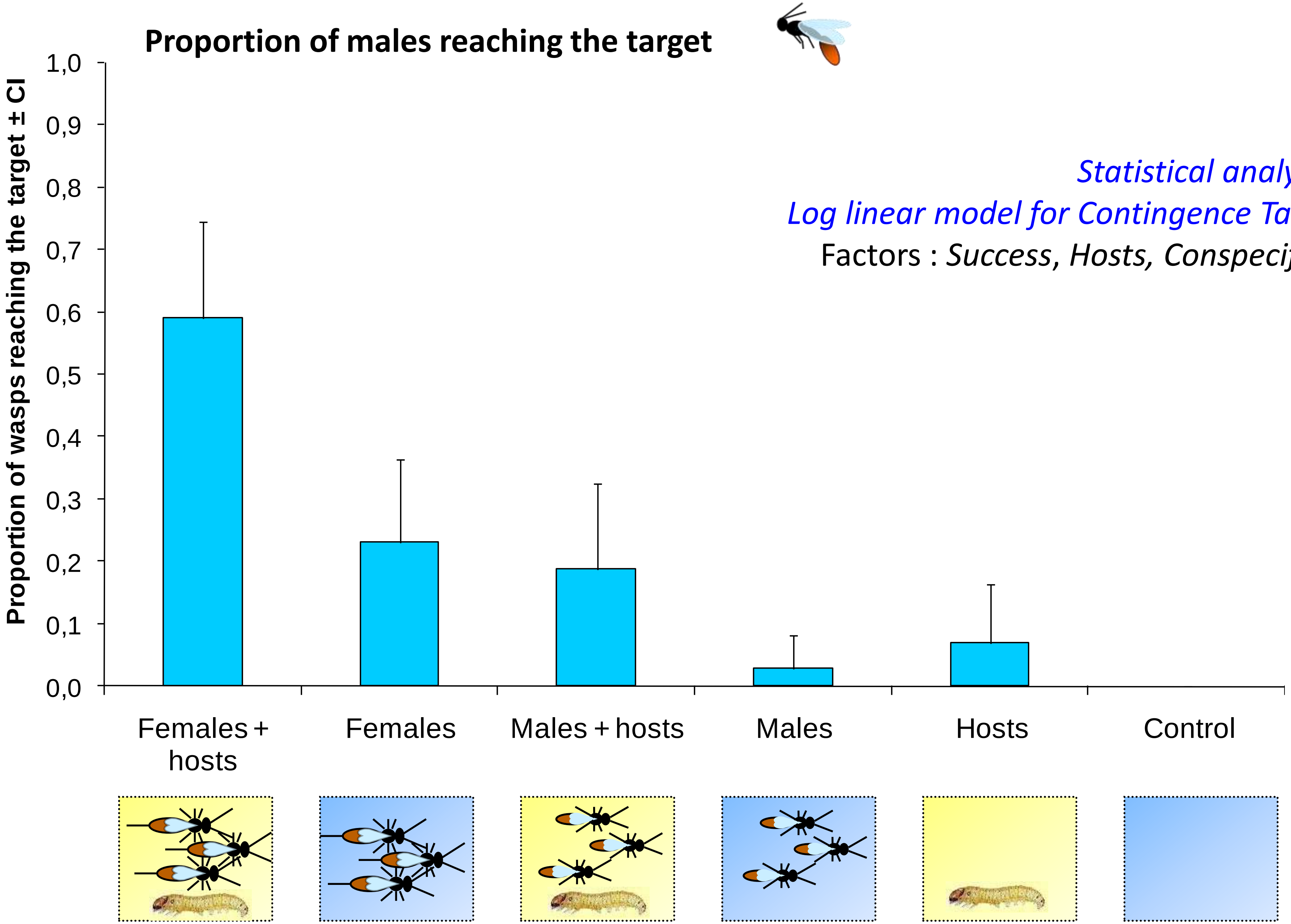
No host

42 replicates by experimental treatment

6 odours so

Proportion of females reaching the target



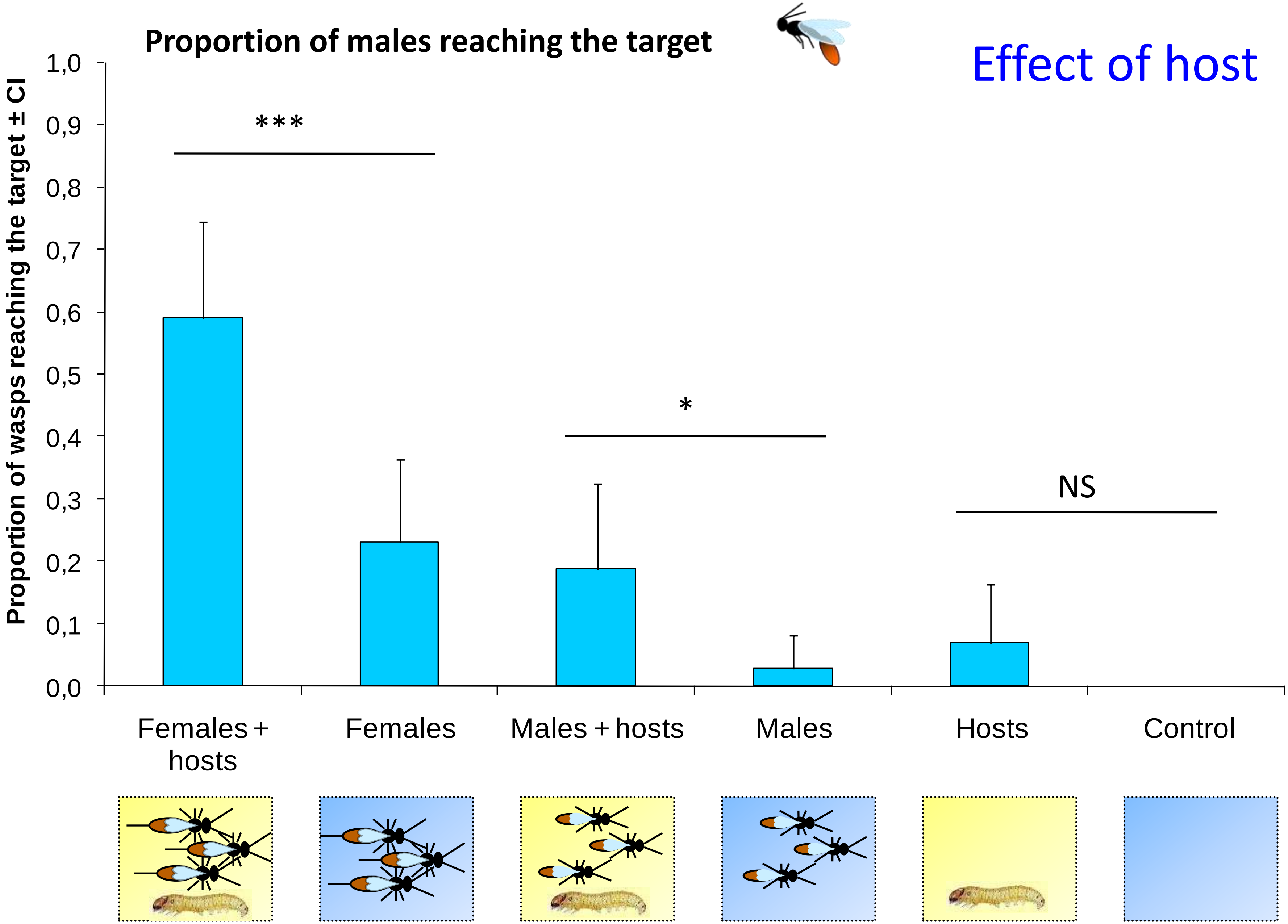


Statistical analysis

Log linear model for Contingence Table

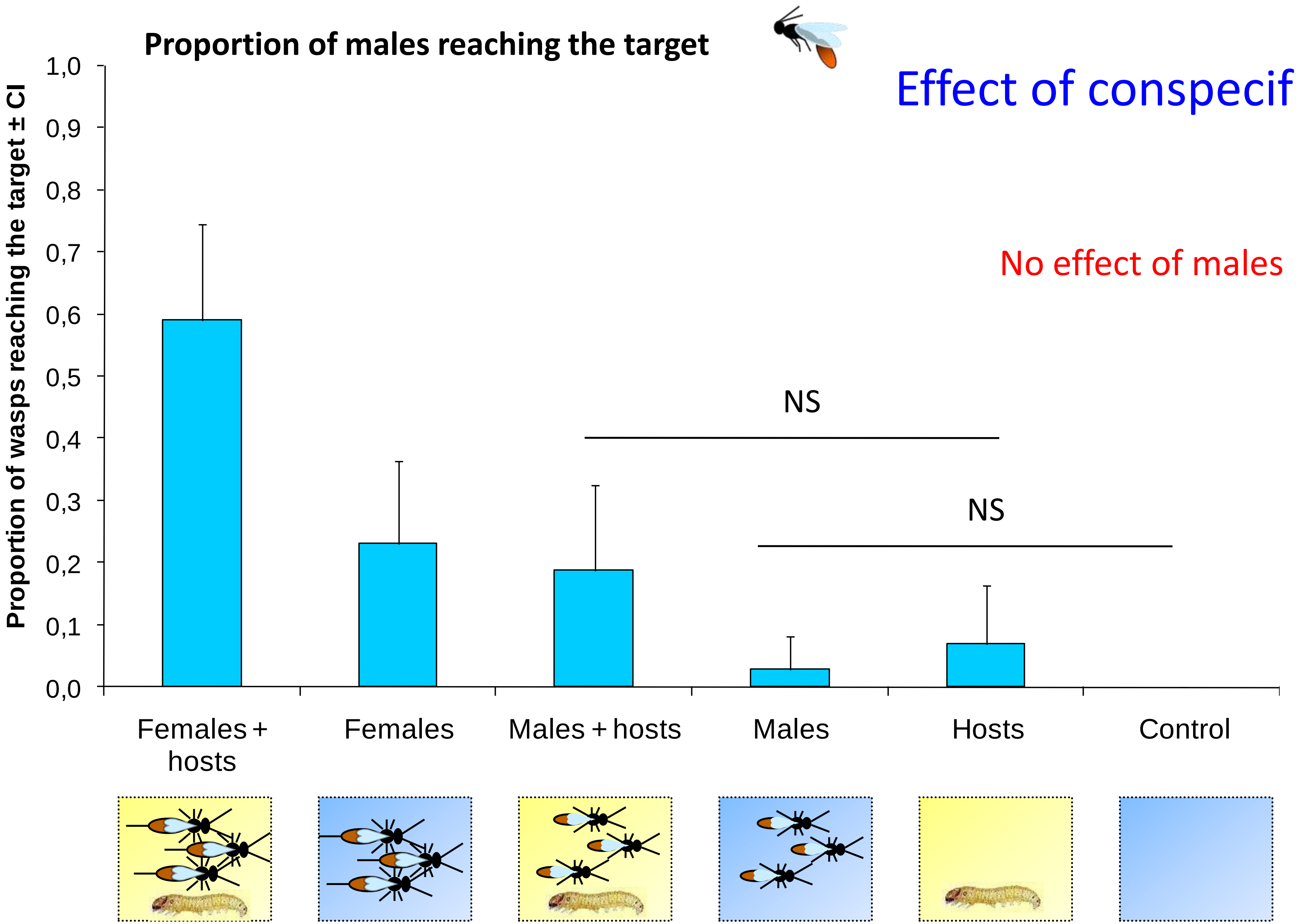
Factors : *Success, Hosts, Conspecifics*

Effect of host



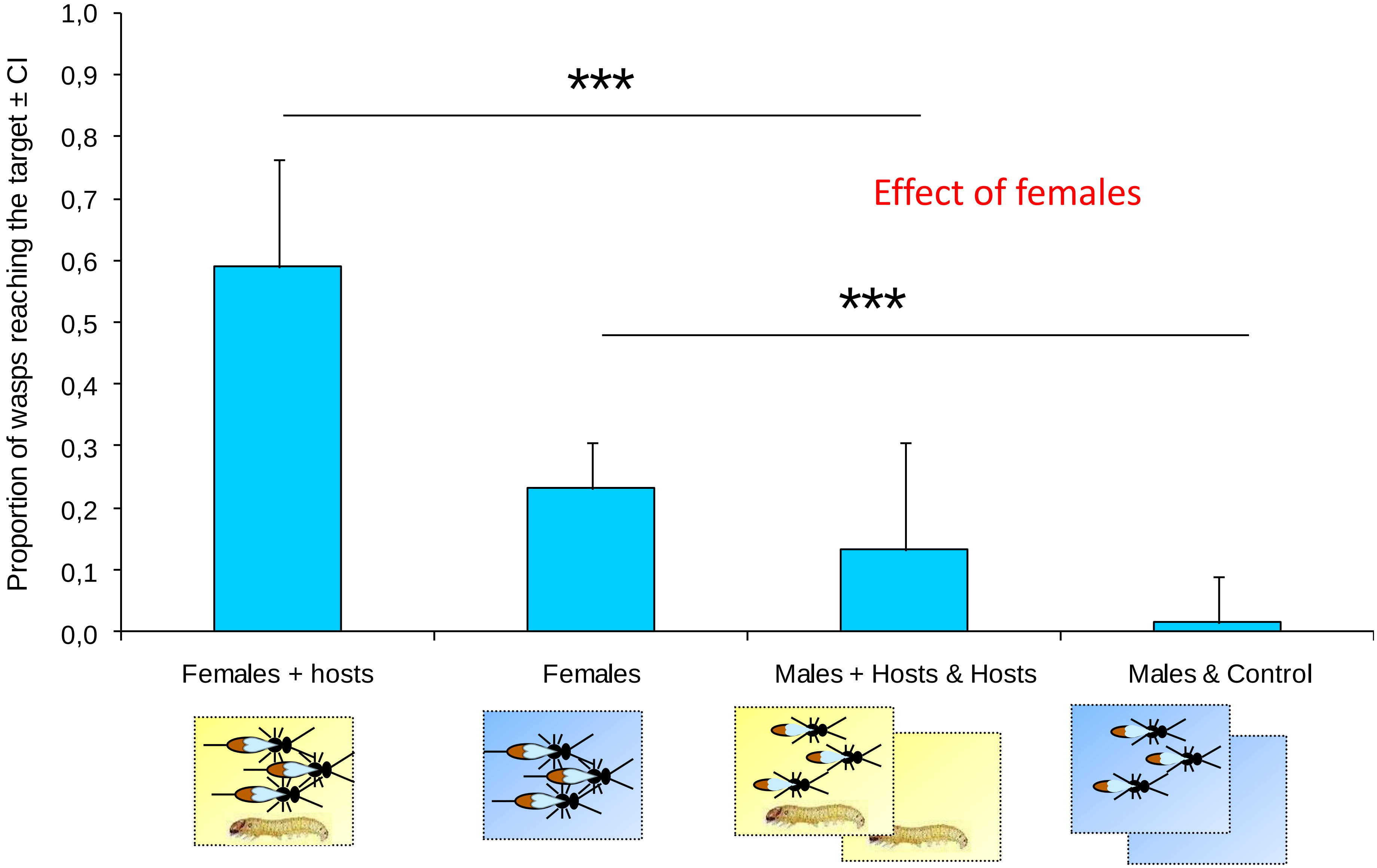
Effect of conspecific

No effect of males

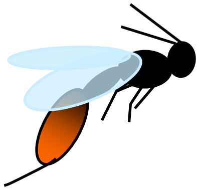


Proportion of males reaching the target

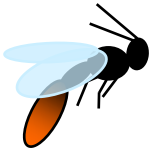
Effect of conspecific



- Summary of results



- females were attracted by host (kairomones)
- they were not attracted by males



- males were attracted by females
- but were not by host
- they were 3 times more efficient to locate females when they were associated with hosts

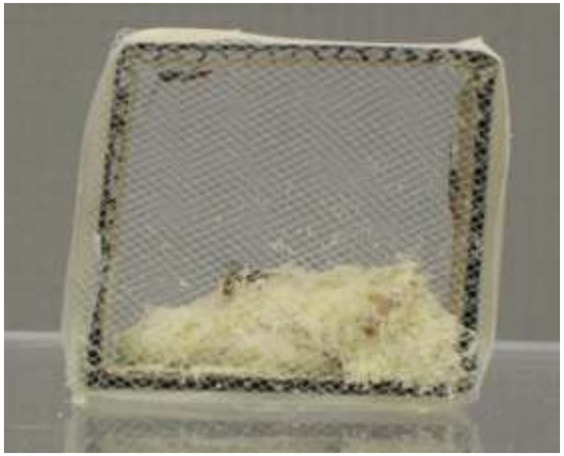
What mechanism explains the increase in female attractiveness when their are associated with hosts ?

- The males are able to combine olfactory information, about females and hosts, to locate the females.

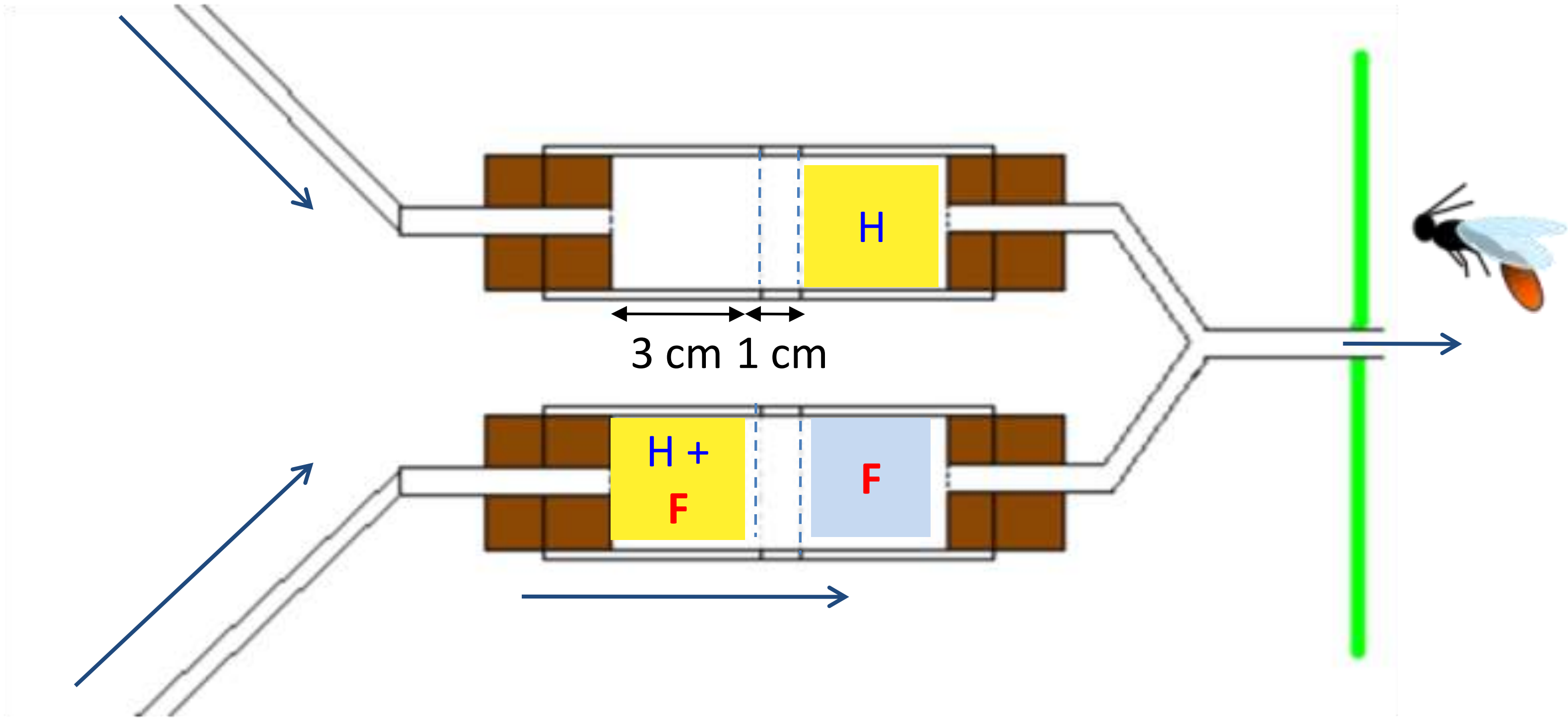
Synergism: effect of the 2 odours taken simultaneously is greater than the sum of their effects taken separately.

or

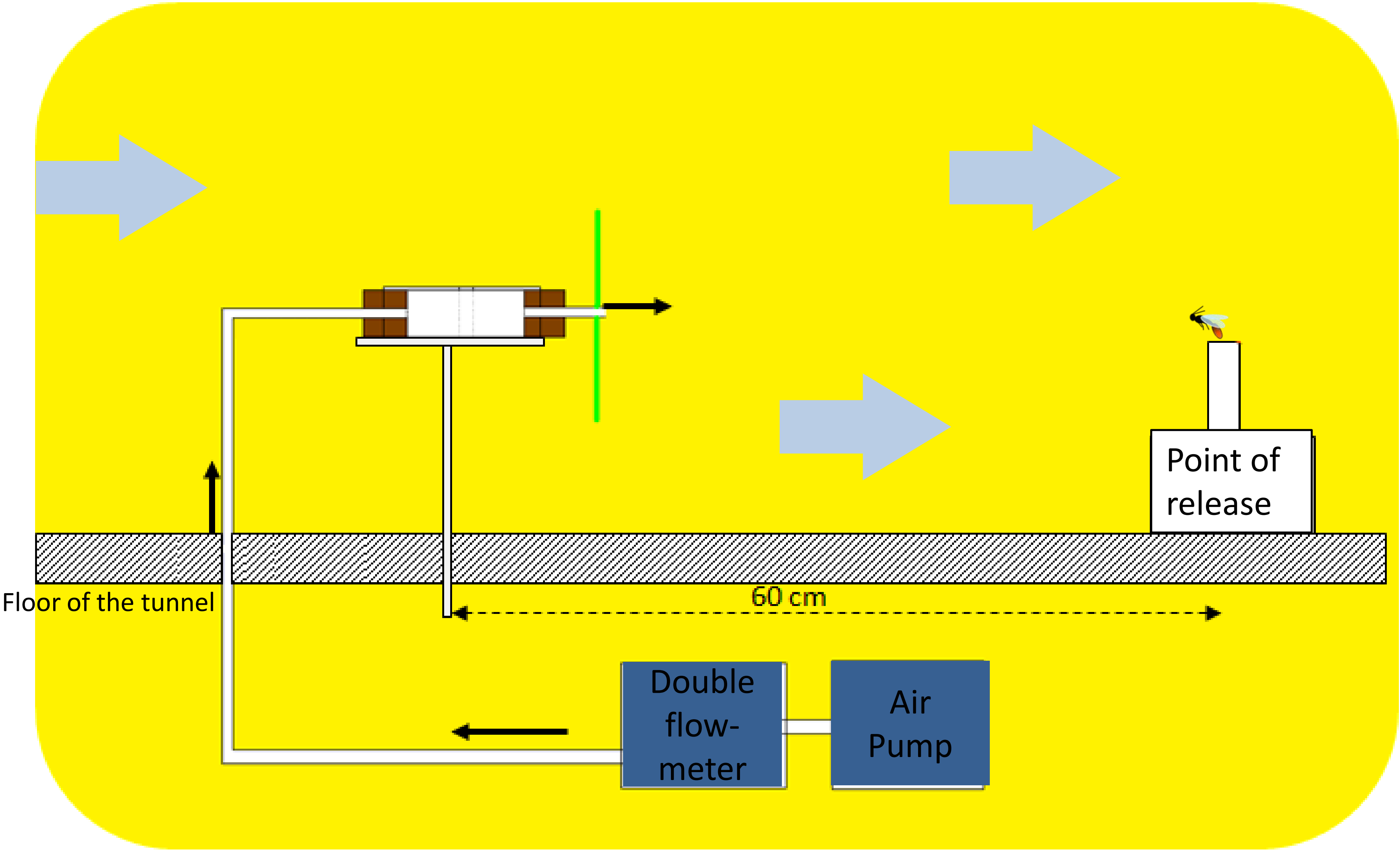
- The females emit more volatiles compounds attractive for males when :
  - They perceive hosts
  - They exploit host patches (oviposition)



Separating odour sources in 4 compartments



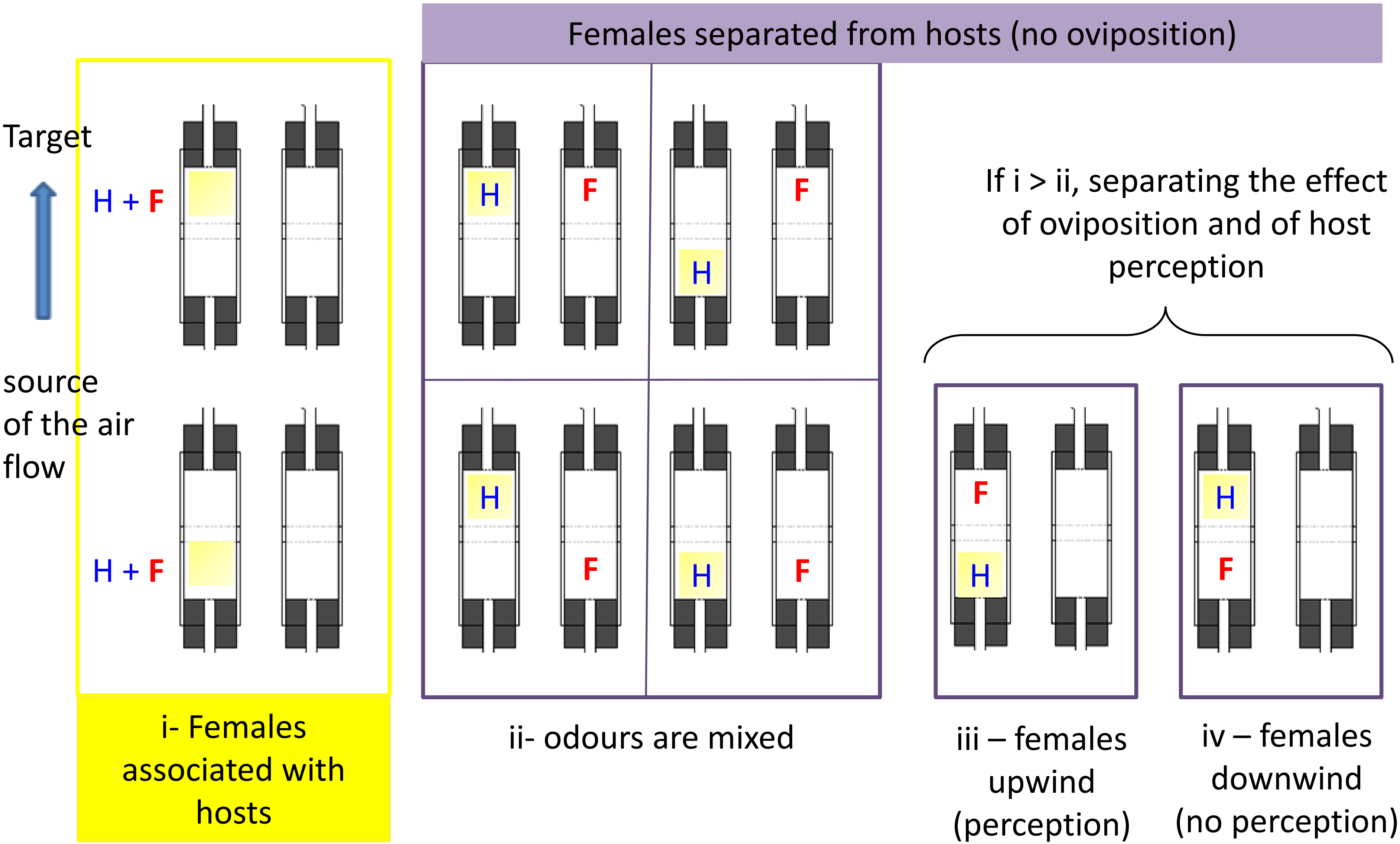
Separating odor sources in 4 compartments



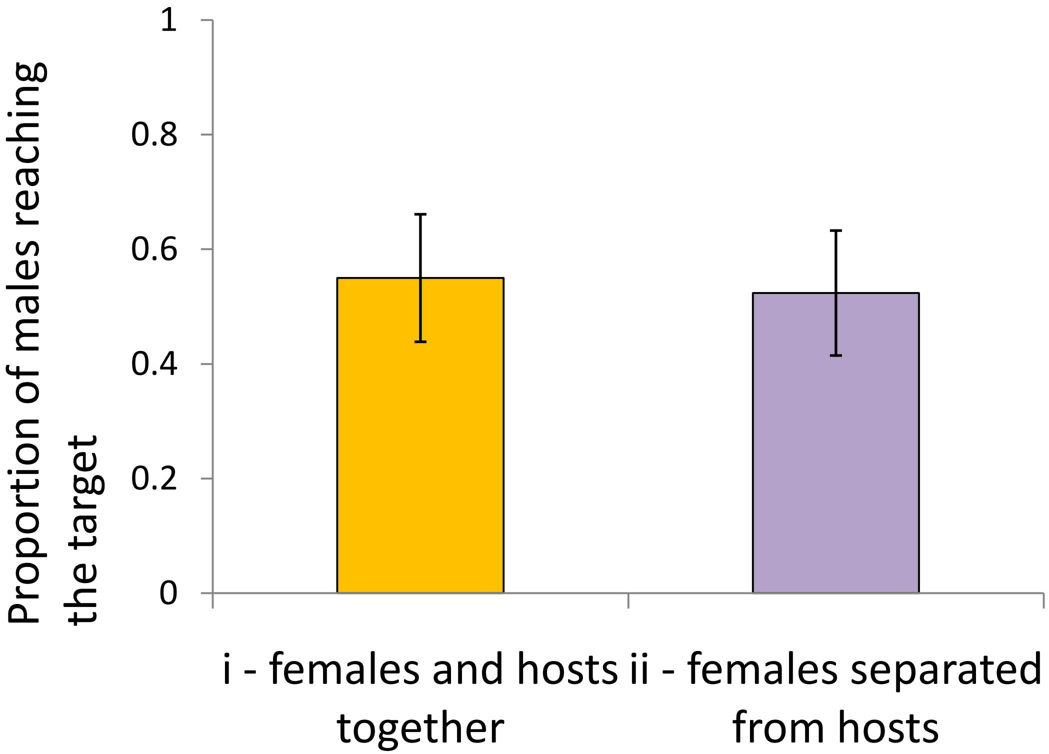
Odour sources tested for male attractiveness

+ left-right inversion

N = 81



No effect of interaction between female and host on the proportion of males reaching the target



Females do not emit more volatiles compounds when they perceive hosts or when they lay eggs

⇒ synergism between odours explain the increase in attractiveness of females when they are associated with hosts

V. canescens : Male and female strategies of mate finding

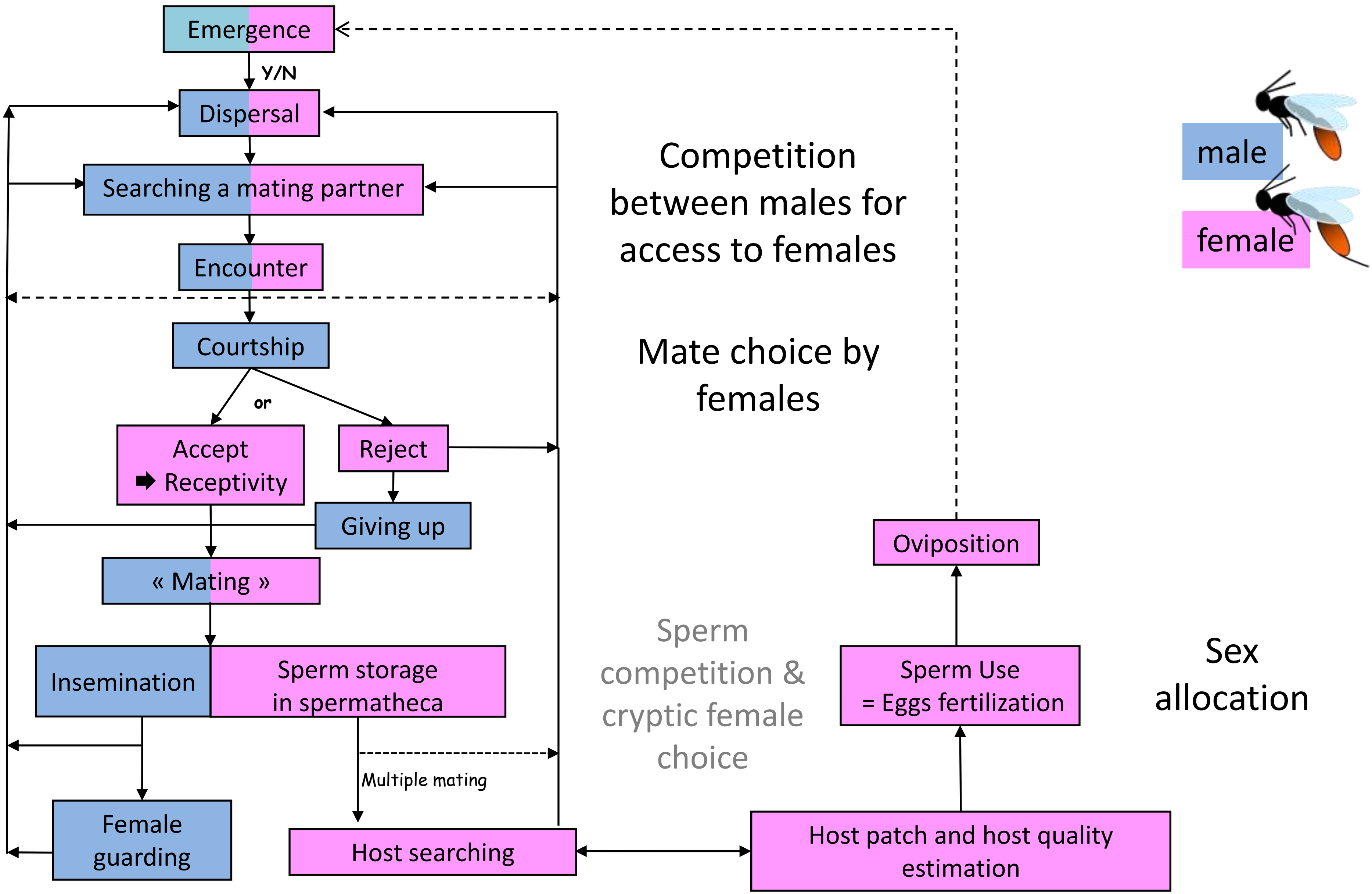
- Males and females may emerge from different places
- Females forage for hosts and food since emergence. They release one or several volatile organic compounds attracting males from a distance (signal = sex pheromone ?).
- Males have to search for receptive (virgin) females
- In this race against other males, they use information on hosts to increase their chance to locate mates : the males are able to combine olfactory information about females and hosts, to locate the females.
- Mechanism : hosts odours (kairomones) act in synergy with female sex pheromone

Part II

Sib-mating avoidance limits risk of genetic incompatibility in a parasitic wasp

Metzger M., Bernstein C. & E. Desouhant. *In prep.*

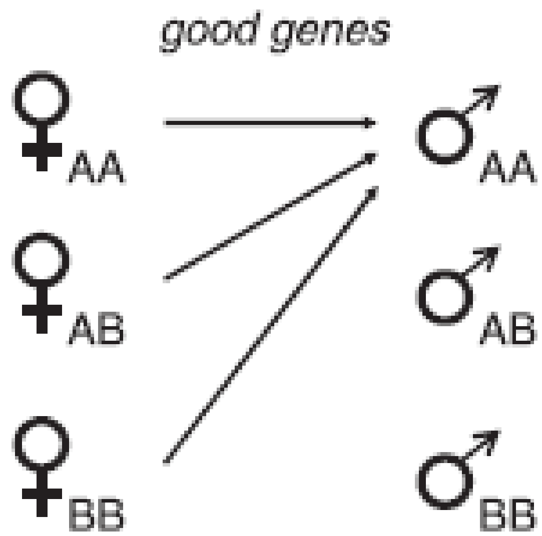
- Mating sequence in parasitoid : chronology of events and decision making



- Criterions of male choice by females ?

can depend on the genetic characteristic of the potential mate

✓ Absolute

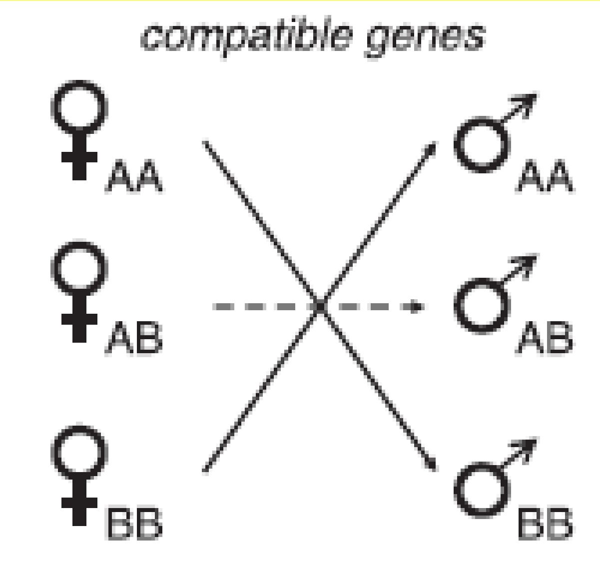


✓ Relative

Allelic combinations ⇒ ↗ or ↘ fitness

Genetic compatibility hypothesis

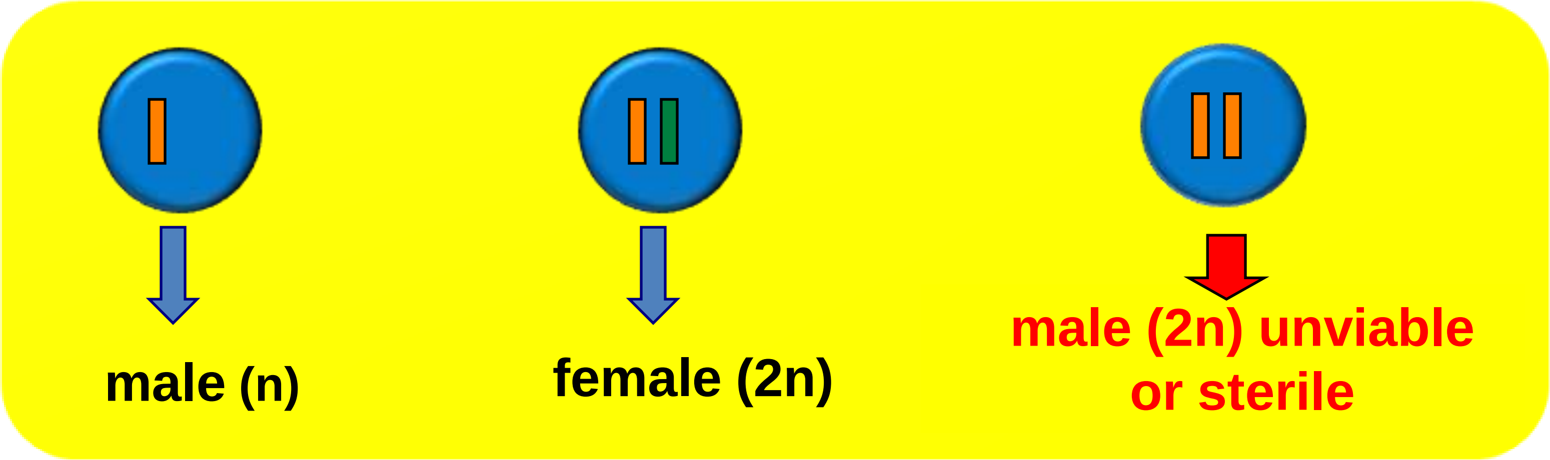
(Trivers 1972, Zeh & Zeh 1996)



- Sex determination system in the Hymenoptera

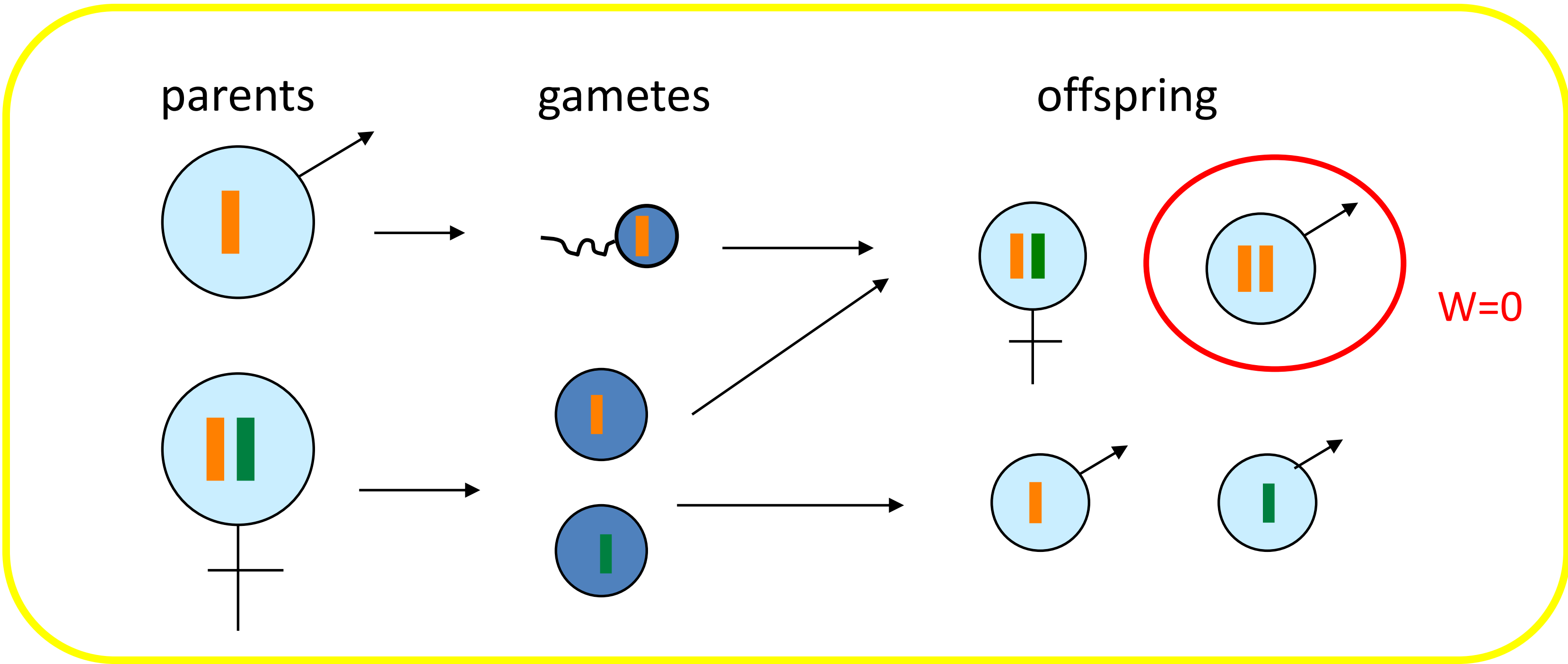
HAPLODIPLOID
males= unfertilized eggs (n)
females = fertilized eggs (2n)

- Sex depend on the allelic composition at a sex locus



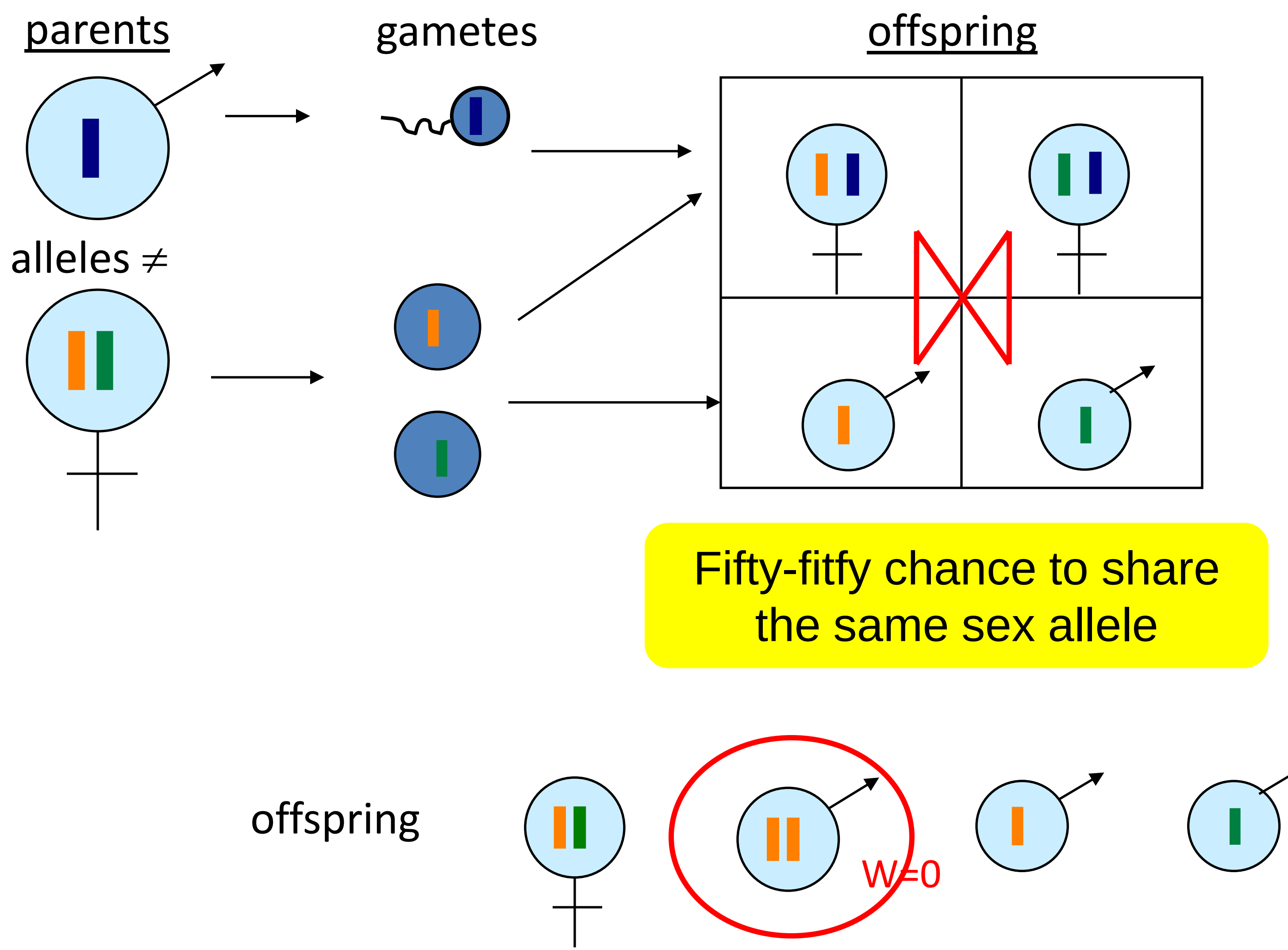
(Single-locus Complementary Sex Determination : Sl-CSD)

- Diploid male production: partners share a sex allele



- Probability of matched mating ?
  - Panmictic population = 2/*k* with *k* the number of CSD alleles
  - Risk increasing with INBREEDING

- Sib mating and risk of genetic incompatibility :



Venturia canescens

- Single locus Complementary Sex Determination (Beukeboom 2001)

- <u>Mating system</u>

  - Monogamous females ⇒ Error is costly

  - Male courtship ⇒ Acceptation or reject = females are choosy

- The risk of sib mating cannot be exclude

- Kin recognition by females : avoidance of superparasitism in host parasitized by related females (Marris et al 1996)

Aim of the study

Does the cost of sibmating have consequences on mate choice in *Venturia canescens*?

Avoidance of genetic incompatibility

Two hypothesis are jointly tested :

- If the probability to encounter a sib male is significant, recognition and avoidance of mating between sib should be selected
- If virginity is costly for females, mate choice decision should depend on age (first mating opportunity late = less selective females)

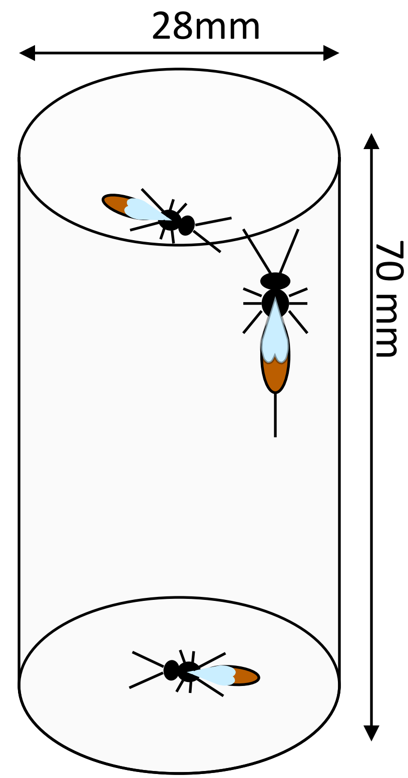
Female's preference for unrelated male ?

4 treatments (*n* = 34)

♀ virgin → 1 day-old → 2 ♂ sib / 2 ♂ non sib

♀ virgin → 4 days-old → 2 ♂ sib / 2 ♂ non sib

(with regard to the ♀)

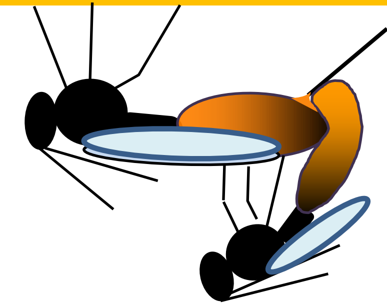


30 min observation

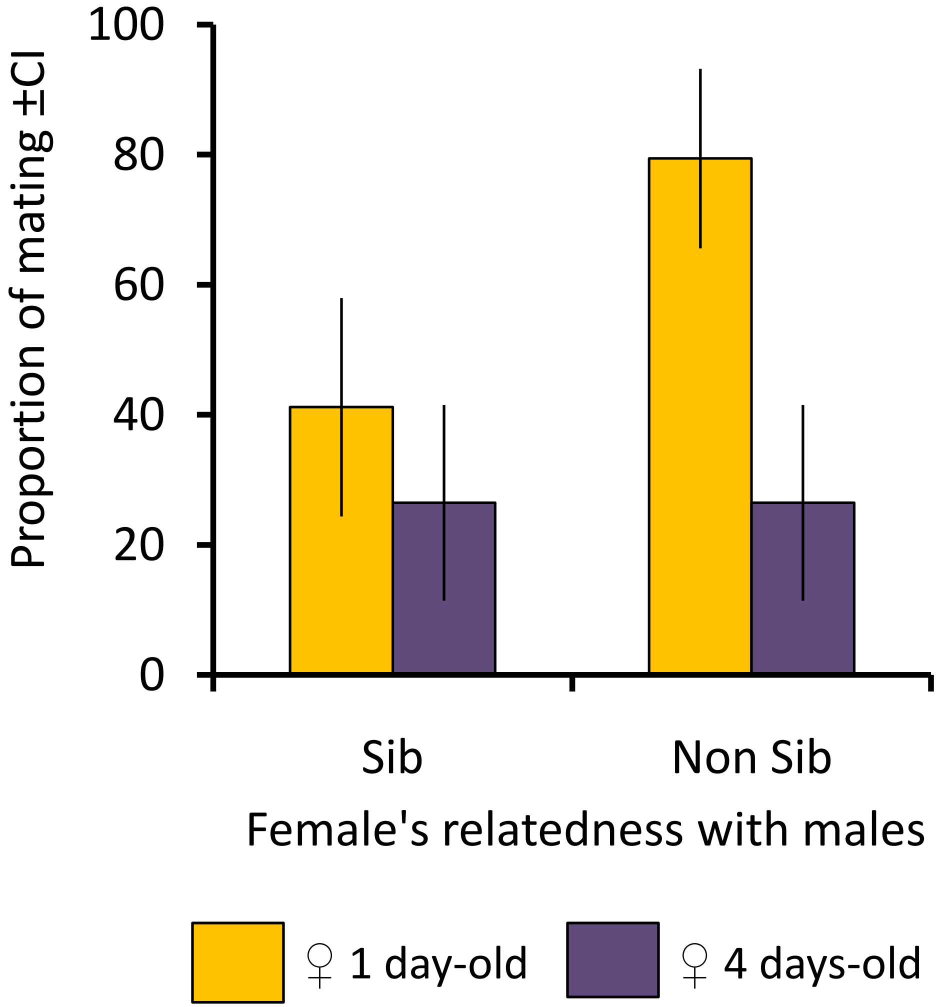
Effect of female age

Effect of relatedness between male and female

on the proportion of mating

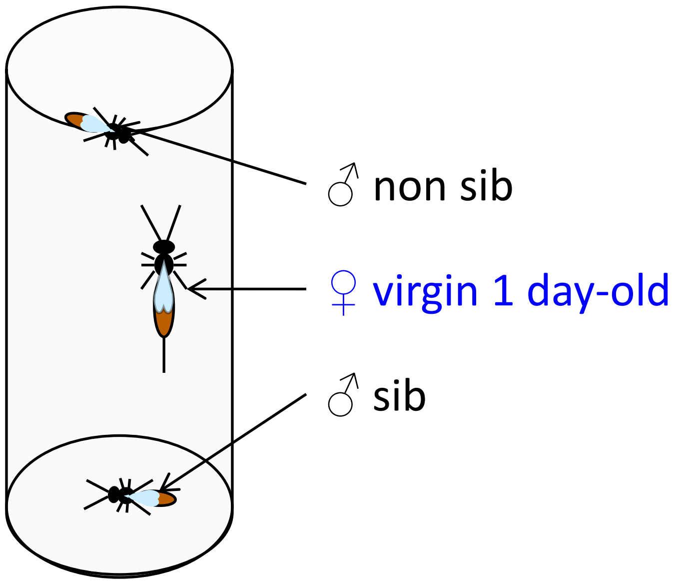


Female's preference for unrelated male



- Young females are selective and prefer mating with non sib than with sib
- With age, females loose their selectivity but accept mating less frequently than younger (receptivity to courtship or attractiveness for males decrease)

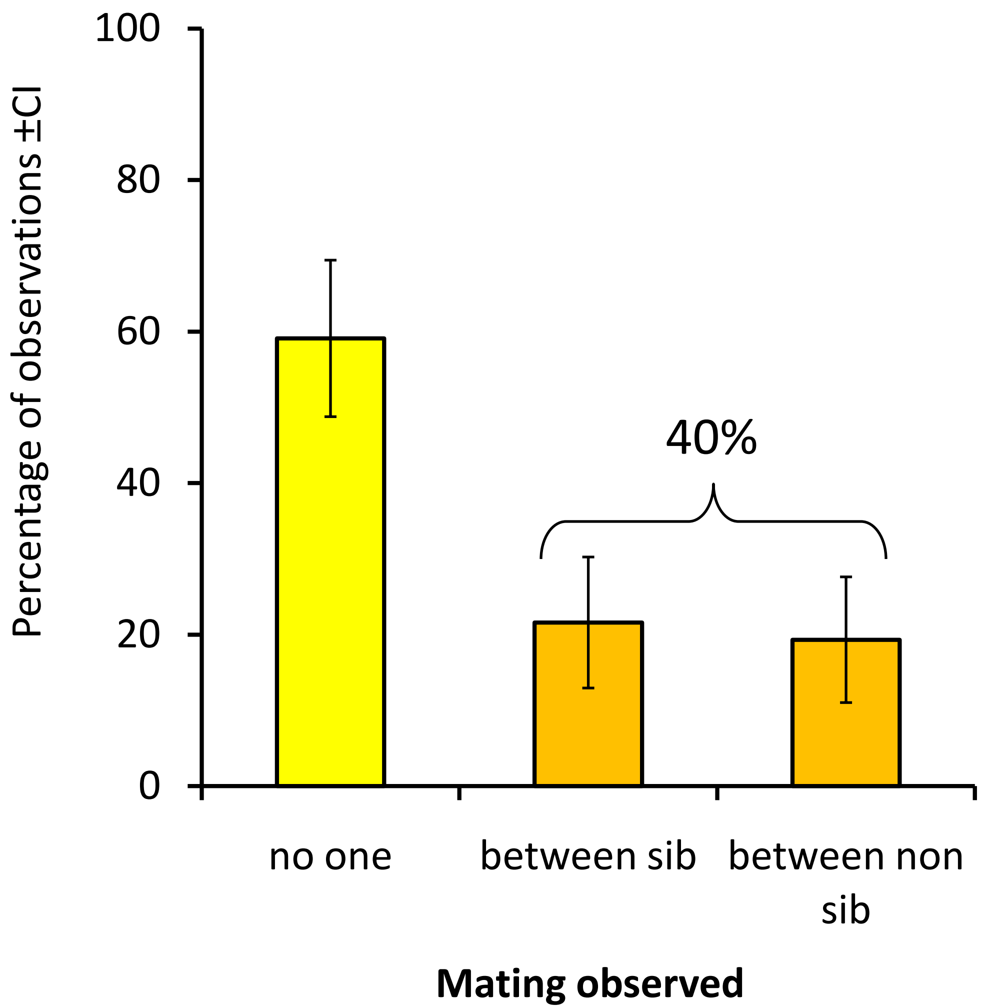
Discriminative ability in a choice situation ?



30 min observation

Proportion of mating and female choice

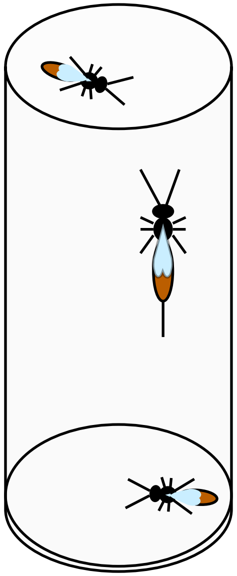
(n = 88)



- First demonstration of sib mating avoidance by kin recognition in a in a parasitic wasp

  Validation of mate choice by avoidance of genetic incompatibility

- In a choice situation between a sib and a non sib, females cannot discriminate sib from non sib males (experiment 2) :



Conflicting results ?

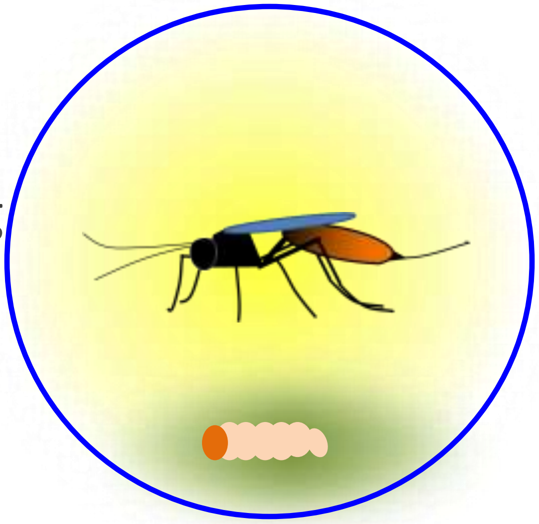
The experimental situation is unfavorable to choice ?

✓ Female is confused between males because of sib recognition mechanism (inhibit receptivity ?)

✓ Effect of the competition between males (« sneaky strategy », Field et Keller 1993)

Discussion
& perspectives

Encounter scenario in *V. canescens*



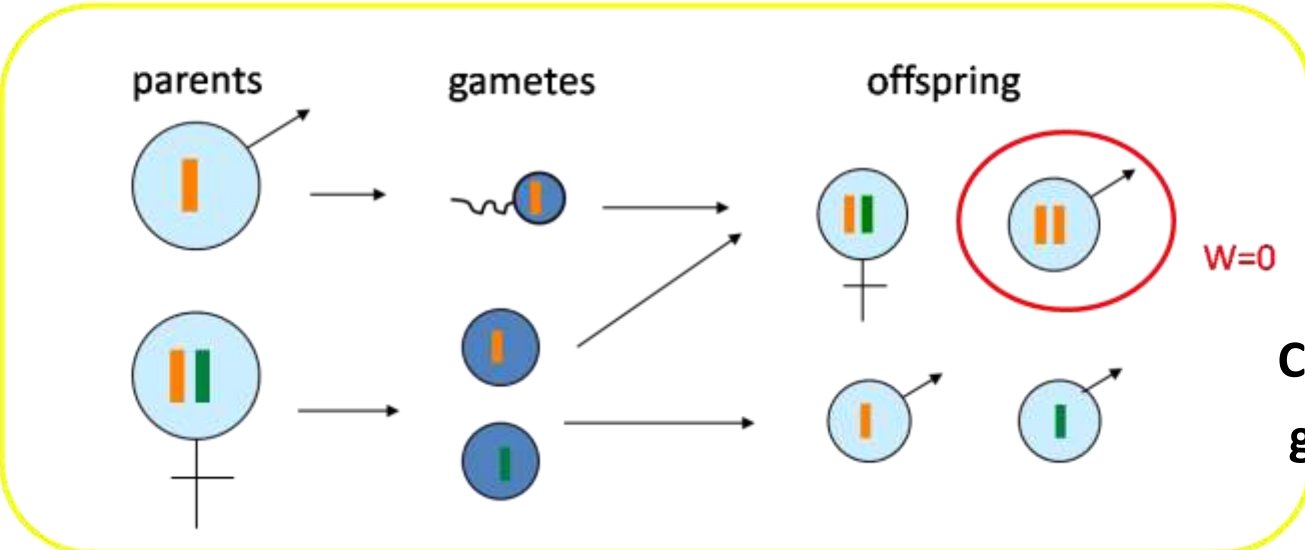
- The males can locate females from a distance using a combination of chemical information:
  - ✓ Pheromonal cue emitted by females
  - ✓ Hosts odour (kairomones)

- Virgin females are caught on host patches in field conditions (Metzger et al 2008)
  → encounter on oviposition site or on natal patch

Neither searching or guarding of the encounter site → Scramble competition between male to obtain mate

Mate choice

- *V. canescens* females recognize and avoid mating with their brothers:



Cost of sibmating :

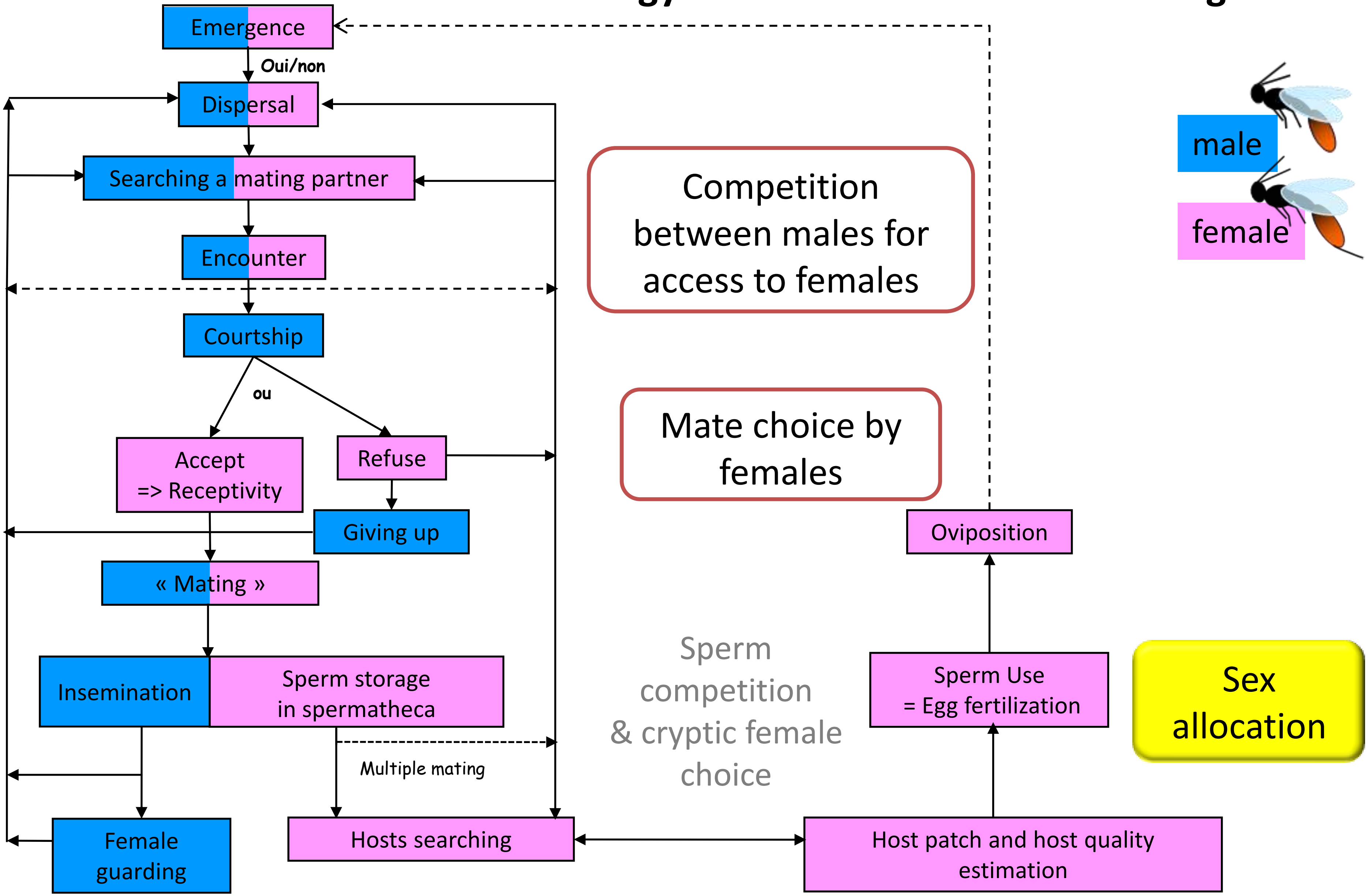
genetic incompatibility

- Possible consequences of sibmating avoidance on parasitoid population :

  ✓ Sex-ratio bias due to increasing time spend constrained by females (Godfray 1990) ?

  ✓ Maintain genetic diversity at the CSD locus : number of sex alleles is a crucial parameter for population stability (Zayed and Packer 2005)

Mating sequence in parasitoid : chronology of events and decision makings



Perspective : which are the underlying mechanisms of mate choice and sib avoidance in *Venturia canescens* ?

- Hypothesis

  ✓ Female recognize an endogenous chemical signature emitted or carried by males : kin template learned by self-reference phenotype matching.

- Chemical ecology experiment is planned

  Aim : to test the hypothesis that brothers odours are closer than non-relative odours.

  Set up : the composition of the volatile compounds emitted (or of male sex pheromone) and of the cuticular hydrocarbons should be determine both qualitatively and quantitatively.

Thank you for your attention

Merci de votre attention