COMMUNICATION CHEMICAL TERMINOLOGY

- **Semiochemicals** are communication chemicals.
- **Pheromones** are chemicals used for communication among members of a species.
- Pheromones are the principal form of communication of honey bees.
- Regulate activities such as colony defense, swarming, and foraging.
- Communicate individual bee sex, caste, and age.
- Communicates nestmate identity, i.e. indicates if an individual lives in a particular colony or not.

CLASSIFICATION OF SOCIAL INSECT PHEROMONES

- Pheromones are classified as **releaser** and/or **primer** pheromones.
- **Releaser pheromones** release a behavioral response that is mediated by the nervous system. Releaser pheromones elicit an immediate behavioral response.
- **Primer pheromones** alter endocrine, reproductive and neurological systems. Changes are not immediate but occur in hours to days.
- Many social insect pheromones are releaser and primer pheromones that are a blend of many components.

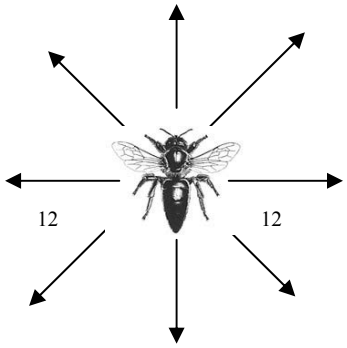
PHEROMONES

- Chemicals are the principal form of communication among insects.
- A simple understanding of the role of pheromones in regulating colony activities such as defense and swarming can help a great deal in understanding beekeeping practices.
- Among solitary insects pheromones are primarily used in mate attraction and comprised of one or two components.
- Among the social insects pheromones are used in mate attraction and much more. Social insect pheromones are often a complex blend of chemicals that have different functions in different social contexts. Pheromone biology is where communication, neurobiology, and physiology interact.

VOLATILE PHEROMONES

- Volatile chemicals usually serve as sex pheromones or mass-action pheromones (defensive).
- Form an odor plume that can be followed along a concentration gradient.
- Majority of social insect pheromones are relatively non-volatile.

NON-VOLATILE PHEROMONES



Volatile space of queen mandibular gland pheromone.

- Non-volatile pheromones have no or short volatile spaces as shown here.
- These pheromones are detected by direct contact with chemoreceptors on the antennae or feet.

RELEASER PHEROMONES

Pheromone	Source	Behavioral Response
2-heptanone	Mandibular gland	Alarm (aggression)
isopentyl acetate	Venom	Defensive (stinging)
Queen mandibular phermone (QMP)	Mandibular gland	Retinue behavior

PRIMER PHEROMONES

Pheromone	Source	Behavioral Response
Queen mandibular pheromone	Mandibular gland	Partial inhibition of worker ovary development
Brood pheromone	Larvae	Partial inhibition of worker ovary development
Brood pheromone	Larvae	Stimulate hypopharyngeal gland development

HONEY BEE SEMIOCHEMICALS OUTLINE

I. Queen Mandibular Pheromone (QMP)

a) Queen mandibular gland
b) Component blend of QMP
c) Mate attraction
d) Species specific blend
e) Racial blends
f) Communicates reproductive status
g) Retinue behavior
h) Pheromone transmission
i) Regulation of colony-level reproduction (swarming)

II. Adult worker bee pheromones

a) Mandibular gland –alarm pheromones
b) Membranes associated with the stinger – defensive pheromones
c) Nasonov gland – orientation pheromones

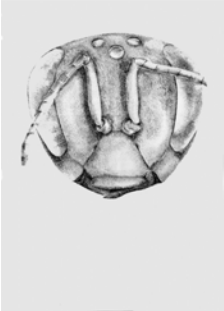
III. Nestmate recognition/discrimination

a) Adults learn the odors of nestmates either as individuals, or as a group (i.e. mixture) of familiar odors and accept individuals that "smell" like nestmates and reject others.

IV. Brood pheromone(s)

a) Cuticular hydrocarbons (fatty acid esters)
b) Communicates caste
c) Communicates stage of development
d) Stimulates hypopharyngeal gland development
e) Releases pollen foraging
f) Dose dependent effects on behavioral ontogeny (affects foraging age of adults)

QUEEN MANDIBULAR PHEROMONE (QMP)



a) Produced by the mandibular glands of queens.

b) **5-component blend of 3 acids and 2 aromatics**.

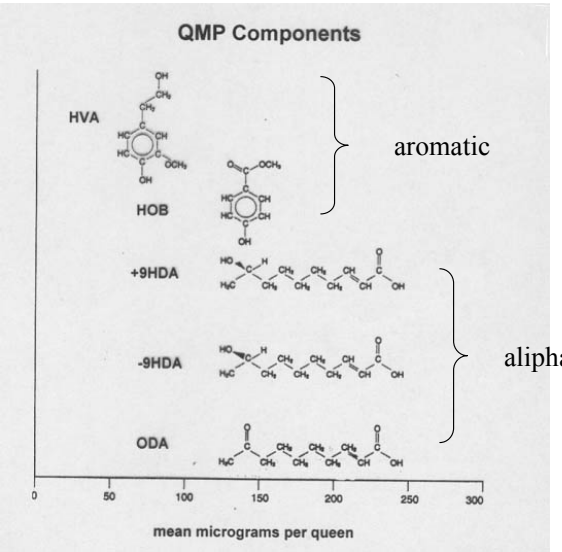
i. ODA; 9-keto 2 (*E*)-decenoic acid (200 µg) .
ii. 9-HDA; *R*- isomer of 9-hydroxy-2 (*E*)-decenoic acid (64 µg).
iii. 9-HDA; *S*- isomer of 9-hydroxy-2 (*E*)-decenoic acid (16 µg).
iv. HOB; methyl p-hydroxybenzoate (20 µg).
v. HVA; 4-hydroxy-3-methoxyphenyl ethanol (2 µg).

- All 5 components in the correct proportions and within a range of amounts are necessary to elicit a retinue response equivalent to whole gland extracts in the proportions and amounts found on the body of a queen.

c) Mate Attraction

1) The most abundant component extractable from the mandibular glands of queens (ODA) attracts drones.
2) Mating takes place in the air and is very difficult to see.
3) Virgin queen blend of ODA is attractive to drones.
4) No bioassays have been conducted to determine what is most attractive to drones.

QUANTITY AND QUALITY OF QMP



QUEEN MANDIBULAR PHEROMONE COMMUNICATES:

1) Species & Race.
2) Queen presence.
3) Continuum of reproductive states; worker, false queen, intercaste, virgin, drone-laying, and mated. Blends of QMP components.

QUEEN MANDIBULAR PHEROMONE DOES NOT COMMUNICATE:

1) Queen age; no known difference in QMP of young and old queens.
2) Fecundity; how many eggs the queen is laying.

SPECIES SPECIFIC BLENDS

Species	Mean amount (µg ± se)			
	ODA	HDA	HOB	HVA
Apis adreniformis (mated)	10.3 ± 3.6	0.3 ± 0.1	-	-
Apis florea (virgin)	1.5 ± 0.5	0.7 ± 0.2	-	-
Apis florea (mated)	0.8 ± 0.1	1.4 ± 0.1	-	-
Apis dorsata (mated)	103.0 ± 41.0	34.0 ± 0.0	-	-
Apis cerana (virgin)	40.1 ± 12.0	2.4 ± 0.5	0.9 ± 0.5	-
Apis cerana (mated)	28.8 ± 6.5	18.1 ± 11.2	6.8 ± 4.5	-
Apis mellifera Euro. (virgin)	108.5 ± 15.0	17.0 ± 22.0	0.34 ± 0.05	0.01 ± 0.01
Apis mellifera Euro. (mated)	207.5 ± 10.6	72.0 ± 5.0	15.6 ± 1.1	2.4 ± 0.9
Apis mellifera Afric. (mated)	96.9 ± 13.4	68.2 ± 10.7	7.1 ± 1.6	1.6 ± 0.4

1) The aromatic components are characteristic of queens from cavity-nesting species; *A. mellifera* and *A. cerana*.

2) *A. mellifera* has HVA and it is necessary for the full retinue response, not so for *A. cerana.*

3) The more derived cavity-nesting species have evolved greater caste-specific differences between queens and workers.

4) Cavity-nesting species have more components necessary to elicit a full retinue response compared to the open-nesting species.

RACE SPECIFIC BLENDS

TABLE 1. MEAN RATIOS OF QMP COMPONENTS TO ODA FOR VARIOUS QUEEN TYPES

Queen type	Ratios		
	9-HDA/ODA	HOB/ODA	HVA/ODA
European mated	0.40	0.09	0.01
Africanized mated	0.75[a]	0.07	0.02
European drone-laying	0.40	0.03[a]	0.002[a]
European virgin	0.20[a]	0.004[a]	0.0004[a]

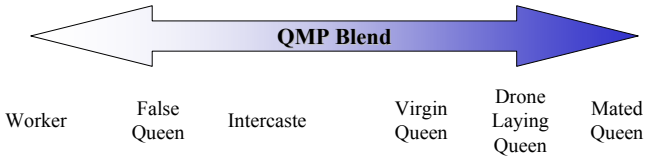
[a]Significant ($P < 0.0002$) difference from mated European queen.

- Africanized queens have proportionately more HDA than European queens.
- 2) HDA is an important component in swarm cluster formation.
- 3) Africanized bees have a higher reproductive rate than European bees. More HDA may be an adaptation for greater reproduction.

OTHER REPRODUCTIVE STATES

1) Egg laying worker: a worker with developed ovaries that is laying eggs.
2) False queen: a worker in a queenless colony that is producing mandibular gland components that elicits some retinue response.
3) Intercaste: individuals that possess some morphological characteristics that are queen- and worker-like.

CONTINUUM OF REPRODUCTIVE STATES CONTINUUM OF QMP BLENDS



QMP BLENDS

- QMP is a blend of 5 components.
- The ratio and quantities in which the various QMP components are presented inform workers about species, race, and mating status.

RETINUE BEHAVIOR

1) QMP arrests workers within the nest resulting in a group of bees surrounding the queen – this is the retinue.
2) Bees aged 7 to 11 days are most likely to engage in retinue behavior.
3) **Retinue bees** contact the queen with their antennae, forelegs, and/or mouthparts.
4) **MESSENGER** bees remove QMP from the queen's body by licking and then **serially transferring QMP from worker to worker** for up to 30 minutes.
5) Retinue behavior transmits QMP throughout the nest communicating queen presence and her reproductive status.
6) All 5 components of the blend are transmitted as a unit.

QMP TRANSMISSION MECHANISMS

1) Movement of the queen.
2) Messenger bees.
3) Retinue bees.
4) Passively through wax.

COLONIES REAR QUEENS TO:

1) Replace a dead queen;
2) Replace an injured or sick queen, and;
3) Colony reproduction called swarming.

QMP

1) Communicates queen presence.
2) Inhibits queen rearing behaviors and physiology.
3) 20 minutes after queen removal reduced levels of QMP are detected by workers.
4) Workers are released from QMP-induced inhibition of queen rearing and queen rearing begins.

QMP REGULATION OF QUEEN REARING

1) Replace a dead queen; QMP regulated.
2) Replace an injured or sick queen; secondary queen cues like amount of larvae more likely than QMP regulation.
3) Colony reproduction called swarming; QMP regulated.

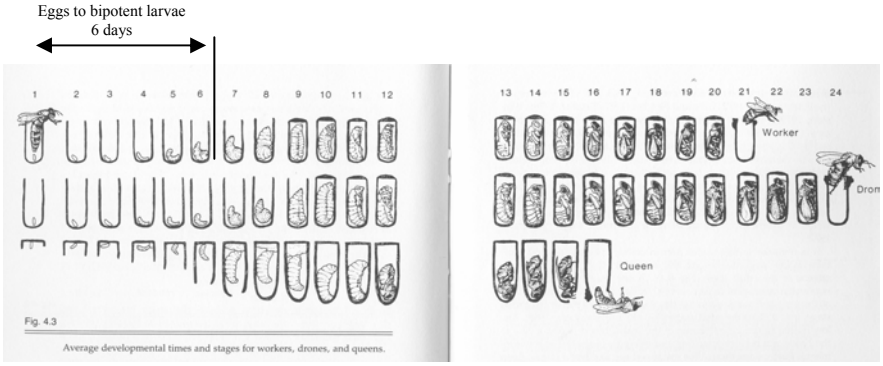
QMP AND COLONY REPRODUCTION

- The principal object of a honey bee colony is to reproduce.
- Colonies reproduce by budding or colony fission.
- As colonies grow to swarming size the amount of QMP in circulation decreases due to a dilution effect.
- Colony congestion also decreases transmission of QMP due to a crowding effect.
- See model of QMP transmission.

PHEROMONE FATE AND TRANSMISSION

1) QMP is distributed throughout the nest by a series of transfers from queen to workers, from the queen to wax comb, and from worker to worker.
2) A worker that licks the queen for up to 60 sec may remove about 11% of the pheromone found on a queen's body.
3) Transmission in the nest approximates a first-order rate equation, meaning that the short-interval transfers are proportional to the quantity present at the source of transfer (all 5 components or QMP travel as a unit).
4) 20 minutes after the queen or pheromone has been removed from the colony, the amount of pheromone circulating decreases below a detectable level. This approximates to the time it takes workers to become agitated after queen removal.
5) 2 hours after removal the amount of pheromone remaining on the comb falls below the worker's level of detection (10-7 queen equivalents). This coincides with the time queen rearing is initiated in queenless colonies.
6) The removal of the queen or the reduced transmission of QMP in the nest due to colony congestion releases bees from queen rearing inhibition and queen rearing is initiated.

7) Within hours of queen loss colonies will initiate queen rearing and have approximately 6 days to choose larvae to raise as queens.



8) Queenless colonies that receive daily doses of one queen equivalent of QMP are inhibited from rearing queens for at least 4 days, but 6 days later they rear just as many queens as untreated queenless colonies.

9) The presence of QMP + bipotent larvae (or an equivalent semiochemical? – hasn't been tested) are necessary to fully inhibit queen rearing.

10) QMP inhibits the initiation of queen cells, but does not inhibit the maintenance of established queen cells.

REGULATION OF COLONY-LEVEL REPRODUCTION

1) Workers are stimulated to produce new queens for colony-level reproduction when: 1) colony size reaches approximately 20,000 workers, 2) the brood nest area is congested, restricting egg laying, 3) the worker age distribution is skewed to a higher proportion of young workers, and 4) there is a reduced perception of the queen's presence.

2) Queen rearing must take place in the presence of the old queen when QMP is in circulation.

3) **Hypothesis:** Transmission of QMP is reduced as the colony grows and becomes congested with increasing worker numbers releasing workers from queen rearing inhibition.

- **Prediction 1:** Colonies given supplemental amounts of QMP while growing to swarming size will show delayed queen rearing and swarming.
- **Experimental Result 1:** Colonies receiving daily doses of 10 queen equivalents (Qeq) of QMP while growing to swarming size swarmed 25 days later than untreated colonies.
- **Prediction 2:** Well distributed QMP will enhance swarming inhibition.
- **Experimental Result 2:** 1 Qeq/day dispensed in a spray delayed swarming for an average of 41 days compared to an average of 25 days for a single-point delivery of 10 Qeq/day.

4) Colony size and hive area have independent effects on the average pheromone levels, but worker congestion has a greater effect on pheromone distribution.

PRACTICAL APPLICATIONS OF QMP

1) As and aid in queen rearing;
   i. Stabilize mating nuclei from worker loss during queenless intervals.
2) To ship queenless package bees;
   i. Sometimes packages are shipped without queens for various reasons (not enough queens, beekeeper want to use another queen source, etc.);
   ii. QMP acts like a pseudo-queen resulting in worker clustering, calmness and hive installation success equivalent to package bees with a queen and superior to queenless packages.
3) Used to delay the timing of swarming;
   i. Buy time for swarm management practices.
4) Used to improve the attractiveness of swarm traps;
   i. QMP + synthetic Nasonov (citral+geraniol+nerolic acid).
5) As an attractant in crop pollination on crops that are not very attractive to bees like pears, cranberry, and blueberry.
6) In disposable pollination units (DPUs). A special technique for using bees to pollinate under certain conditions. DPUs are small colonies with no queen, designed to be left at the crop for pollination then discarded.
7) Research tool.