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PP-436 [Bee Biology]

Where do Honey Bees Mate?

Dr. Gard W. Otis

Institute of Bee Health, University of Bern, Switzerland
and
School of Environmental Sciences, University of Guelph, Canada

Background

It is generally accepted that to mate, (i) drones leave their colonies and fly to a drone congregation area (DCA) where they await queens; (ii) queens fly to DCAs; and (iii) most (if not all) matings occur within these aerial aggregations of males.

This view of mating behavior has emerged from discovery of DCAs on every continent where *Apis mellifera* occurs and occasional observations of queens mating in DCAs.

Problems with this interpretation of mating behaviour are:

- Some matings have been observed outside of DCAs, along routes drones follow ("flyways") through the landscape or near their hives.
- DCAs do not exist in flat, featureless landscapes with few landmarks.
- In some landscapes, drones are attracted upwind to queen pheromone lures for 60-300+ m.
- Drone tracking by radar indicates that:
  - Drones fly from their colonies along fairly linear paths ("flyways") that follow landmarks; where a flyway bends, branches, or terminates, they fly higher and rapidly change directions in what look like DCAs; *therefore,* ***DCAs may be reorientation points*** as drones navigate across the landscape;
  - Drones fly further as they age, presumably as they become familiar with landmarks in the landscape (O.R. Taylor & G. W. Otis, unpublished research).
  - Drones do not wait in DCAs for queens; they fly from one DCA to the next.
- We have never been able to track queens on their mating flights, so there has been no unbiased and systematic research on where queens go on mating flights.

Left: Comet of drones in pursuit of a queen; courtesy of Pierre Giovenazzo.

Right: Drone attempting to copulate with a queen; courtesy of Markus Imhoof, "More than Honey", and Boris and Barbara Baer-Imhoof, University of California, Riverside.

Review of statements in the literature about where honey bees mate

My review of the literature found 158 refereed journal articles, 42 books and 3 theses with statements about where honey bees mate. I scored them in four categories:

S = definitive statement that matings occur in DCAs;

I = statement that implies that matings occur in DCAs:

E = equivocal wording about where mating occurs;

N = neutral: mating frequencies across the landscape match local drone densities.

The results of my analysis of the literature are:

	S	I	E	N	Total
Pre-1997	12 (23.1%)	20 (38.4%)	15 (28.8%)	5 (9.6%)	52
1997-present	125 (82.8%)	18 (11.9%)	5 (3.3%)	3 (2.0%)	151

- **Conclusion:** most researchers have accepted that queens and drones mate predominantly in DCAs (**S** + **I**) despite a lack of proof.
- This belief has become entrenched over time.
  - Prior to 1997, *61.5%* of sources stated or implied that DCAs were the sites of mating.
  - From 1997 to July, 2025, that percentage increased to ***94.7%*** of published sources.

Evolution of viewpoints over time (Italics added for emphasis):

Roger A Morse:

- "... definite drone congregation areas exist, and *it would appear* that queens search out these areas and are there pursued by drones" (Zmarlicki & Morse, 1963). (Note: no queens were observed in that study.)
- "*The fact* that drones and virgin queens fly to specific areas, now called drone congregation areas, for mating, was discovered by Zmarlicki" (Morse & Hopper, 1985).
- "… *generally queens fly to areas called 'drone congregation areas*.' These are locations where the males congregate and apparently wait for the mating queens" (Morse, 1986).

Friedrich Ruttner:

- "*We must assume* that matings take place in the drone congregation areas" (Ruttner, 1996).
- "*It was not proved for sure but it is likely* that most queens mate in the drone congregation areas" (Ruttner, 1972).
- "*The assumption* that queens mate mainly in drone areas is supported by…" (Ruttner, 1986).
- "The queen risks her life on *mating flights, which drive her to the drones' courtship grounds. The entire male population of the region assembles 'in certain gathering places in the sky'"* (Ruttner, 1992).

Recent shifts that recognize how little we know about where honey bees mate:

- "Whether these [DCAs] are actually mating hot-spots is *yet to be proven*, but they have similar properties to other species' mating swarms" (McAfee, 2021).
- "There is *conflict* over whether drone congregation areas are truly sites of mating in a natural setting or are instead convenient locations for researchers to find drones" (Metz & Tarpy, 2022).

Where do we go from here?

Researchers have demonstrated that drone behavior is influenced by:

- Landmarks or lack thereof (DCAs do not form in featureless landscapes);
- Topography (drones follow valleys and fly further in mountainous regions);
- Drone density (distinct DCA boundaries at low drone density disintegrate at high density);
- Magnetic fields and drone pheromones (both affect drones in flight, but by how much?)
- Queen mandibular pheromone (drones are attracted upwind from flyways to queens and queen lures, but how far seems to vary between sites and studies).
- Weather (DCAs form in the lee of hills or large trees in windy weather).

There have never been controlled experiments to test the the effects of these factors on drone behavior; consequently, we have a poor understanding of them.

- In 1892, Gilbert Doolitte wrote: "If drones congregate in certain places, it would be but natural that the queens should be drawn to these places; and the fact that one queen was known to mate at such a congregation of drones went quite a way with me in leading me to believe that queens in general were so mated."
- That logic seems to have been adopted by most honey bee researchers **in the absence of unbiased information on where queens mate**.
- **Most matings may occur in DCAs but there have been no studies that demonstrates that.**

Why is it important that we learn where mating occurs?

- Considerable research has gone into trying to understand where DCAs occur, but it has little application to beekeeping because queens fly unknown distances to mate with drones from the surrounding 50 km².
- Queen producers and beekeepers who rear their own queens would like to maximize the mating of their queens with desired drones.
- If we do not know where mating occurs, or how far queens and drones fly on their mating flights in various landscapes and at different densities of drones, we cannot place drone source colonies in the best locations and numbers to exert the best influence on matings.
- **DNA-analyses can be used to determine purity of queen matings under various conditions.**

We currently lack the technology for long-distance tracking of individual drones and queens. When that technology becomes available, we will finally learn where honey bees go to mate.

For a detailed review of honey bee mating, go to:

Otis, G.W. (in press). Where do honey bees (*Apis mellifera*) mate? *Apidologie*

PP-436 [Bee Biology]
Where do honeybee queens mate? A critical review

Gard W. Otis
Institute of Bee Health, Agroscope, University of Bern, Switzerland

We have known for 250 years that honeybee queens and drones must leave their nest to mate. Evidence began to surface 100 years ago that drones congregate in the air on their mating flights. With the discovery in the 1960s that drones in some aerial locations within the landscape could be attracted to queens or queen mandibular pheromone, it became possible to search for "drone congregation areas." It was subsequently assumed by most researchers that DCAs represent mating swarms of drones, with many authors claiming, without direct evidence, that drones and queens orient to DCAs where matings occur. It is frequently implied that DCAs have evolved specifically for the purpose of mating.

There are several issues with this generally accepted explanation that mating occurs exclusively in DCAs. (1) In relatively featureless landscapes, drones are reported to fly randomly through the landscape and DCAs do not exist. (2) When drone flights have been tracked with radar, drones move from one aggregation site to the next along flyways, and fly to more distant DCAs (and not the same DCA repeatedly) as they age. (3) Where drone densities are extremely high (e.g., in commercial queen mating yards), queens have been observed to mate very quickly and close to their hive. (4) Few people have observed matings, some of which occurred outside of a DCA. An alternative, neutral hypothesis is that honeybee mating frequency is dependent on landscape features and drone densities: queens mate wherever they encounter drones.

I have extracted statements concerning the location of mating from nearly 200 scientific articles and books. In my presentation, I will summarize these data and review the evidence for and against DCAs as mating sites. In my opinion, we actually know very little about where queens mate. This uncertainty will be resolved only when queens can be fitted with tiny transmitters and tracked on mating flights within a landscape in which the densities of flying drones and locations of DCAs are known.