

Johnson et al., 2013



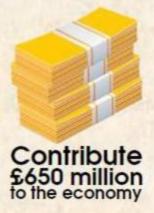
- There are over 20,000 species of bees.
- Bees of all varieties live on nectar and pollen.
- Without bees, pollination would be difficult and time consuming - it is estimated that one-third of the human food supply depends on insect pollination

ALL BEES



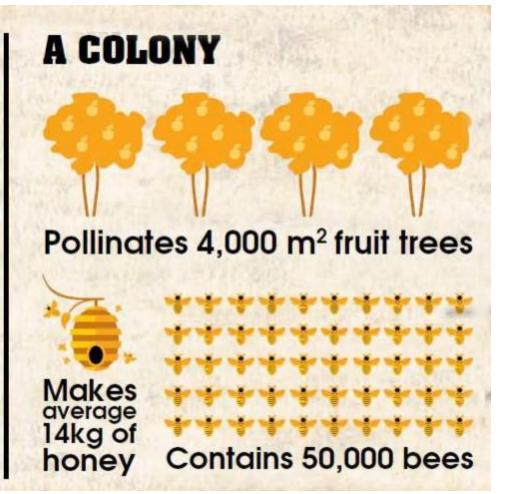
Estimated 1/3 of food is pollination dependent







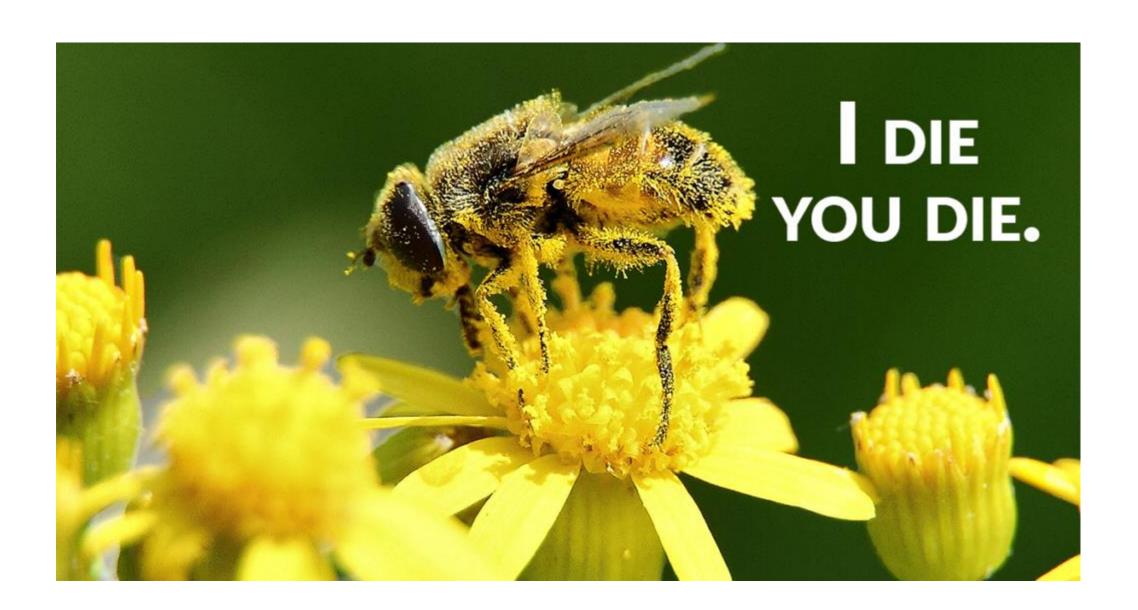
Pollinate 70 types of crop













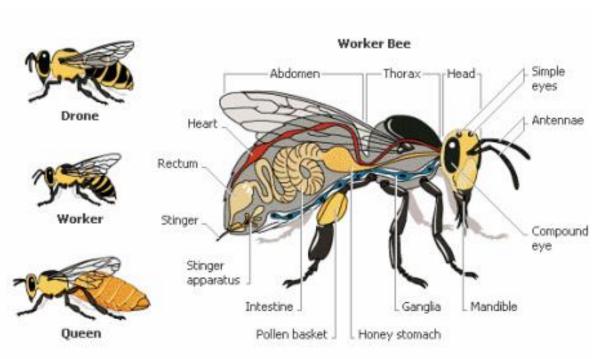
Apis cerana hive





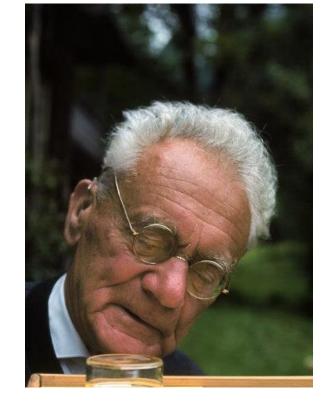


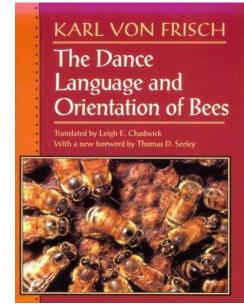
Apis florea hive





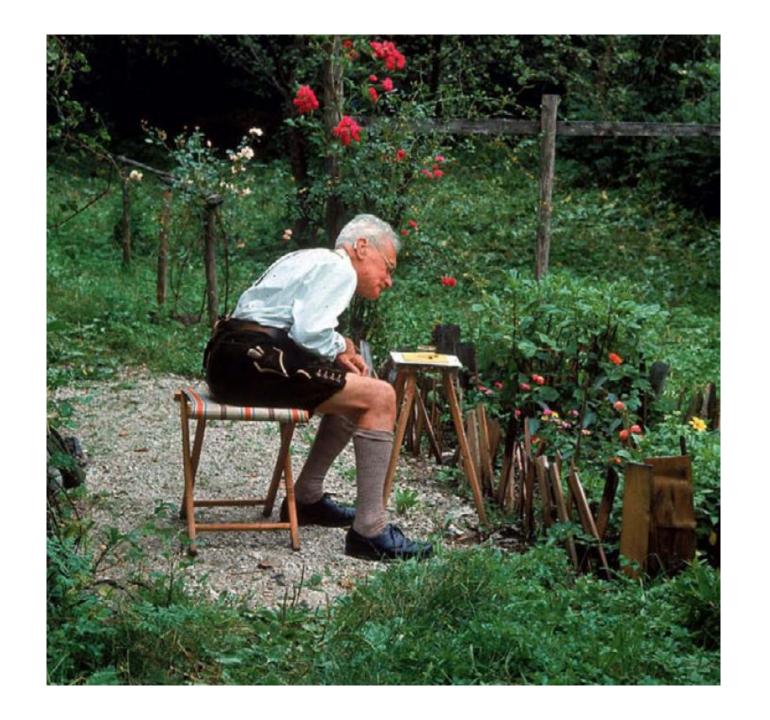
- It has been known for centuries that honeybees must pass information about flower crops to one to another.
- However, this communication system was largely uncovered by the Austrian Zoologist, Karl von Frisch.
- For over 20 years he slowly uncovered this mode of communication.
- The conclusions that he came to were so extraordinary and unparalleled that he himself declared that no good scientist should accept them without confirmation.
- Following World War II, other zoologists did confirm von Frisch's results and even worked with him on some final experiments.





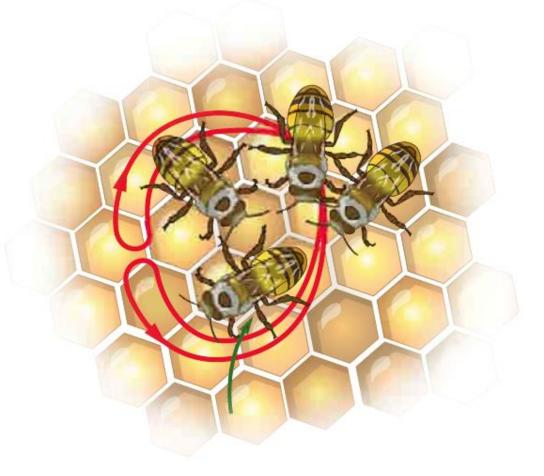
- von Frisch had noted that if a source of sugar solution was put out to attract bees it was often many hours before the first one found it, alighted and drank.
- However, once a single bee had located the source it was usually only a matter of minutes before many other foragers arrived – somehow the information had been passed on.
- Von Frisch marked foragers on their thorax with a tiny spot of paint as they drank at a dish of sugar syrup and then watched their behaviour when they returned to the hive.





- The forager usually contacts other bees on the vertical surface of the comb and gives up her cropful of sugar solution to them.
- Then she begins to dance.
- If the food is nearby (within 50m) she performs a round dance.
- Her dance then is rapid in tempo and forms a roughly circular path just over her body's length in diameter.
- The bee moves in circles alternately to the left and to the right. She stays approximately in the same place on the comb and may dance for up to 30 s before moving on.
- Other foragers face the dancer, often with their antennae in contact with her body, and follow her movements closely, being themselves carried through her circular path.

- This round dance stimulates other workers to leave the hive and search nearby.
- It appears to convey the information, 'search within 50 m'.
- It may also convey some olfactory cues, because if the food source is scented the dancer will carry this scent on her body and perhaps in the sugar solution itself.
- If the sugar dish is not scented the forager may mark it to some degree by opening the Nasanoff scent gland on her abdomen as she drinks.



The 'round dance' of the honeybee worker on the vertical face of the comb. Her path is indicated by the lines

- Thus far the bee dance is not very exceptional, because many ants and termites have similar alerting displays and pheromones which help to organize foraging activity when a new food source has been found near the nest.
- The extent of the honeybees' communication system is not revealed until the food source discovered by a forager is further from the hive, beyond 100 m.
- Von Frisch observed that as his food dishes were moved beyond 50m the forager's round dances gradually changed in form.
- short straight run became incorporated between the turns and on this run the dancer wagged its abdomen rapidly from side to side.
- At about 100mdistant the dance had become the typical 'waggle dance'. And this form remained the same as the dish was moved further, to 5km or even beyond.

Watch video 1

https://www.youtube.com/watch?v=LU_KD1enR3Q

- It is this waggle dance which, von Frisch claimed, transmits so much more information and is 'read back' by the dance followers as they follow every move the dancer makes.
- The waggle dance certainly does contain information about both the distance and the direction of the food source.
- Distance is correlated with several features of the dance.
- Von Frisch concentrated on measuring its tempo, which falls off with distance, steeply at first and then more gradually.
- There are 9–10 complete cycles per 15 s with the food at 100 m, but only 2 when the food is 6km away.
- The duration of the waggle run, the number of waggles it contains and the duration of the sound pulses also correlate with distance, all three features increasing with it.

- It is its relation to the direction of the food source which is perhaps the most remarkable feature of the waggle dance.
- Occasionally honeybees will dance on the flat landing board (horizontal surfaces) provided at the entrance to most types of hive. If they do so, then their dances also point directly to the food source.
- However, inside the hive most bee dances are on vertical surfaces.
- Von Frisch noted that the average direction of the waggle run was consistent within a dance and that it was the same for all the foragers who danced after feeding at the same dish.
- Given that other bees foraging at different dishes made waggle runs orientated at other angles even when the distances were comparable, this was strong circumstantial evidence that the angle related to direction in some way.

- Now came the crucial observation!
- von Frisch recorded dance after dance throughout the day as foragers repeatedly returned from the same food source and he found that the direction of the waggle run gradually changed. Its mean direction shifted by about 15 degrees per hour and this could mean only one thing: that it relates to the apparent movement of the sun.
- The foraging bee, like many other insects, uses the sun as a compass and records the position of the food source with respect to it.
- To get to the food it steers, say, 40 degrees to the right of the sun. When dancing on the vertical comb the sun is not visible but the bee transposes the angle to the sun into the same angle with respect to gravity.
- The honeybees' 'convention' takes vertically upwards to represent the present position of the sun.

- Thus the forager dances with her waggle run 40 degrees to the right of vertical.
- As her course with respect to the sun will have to change as the day progresses, so she changes the angle with respect to gravity on the comb to match the sun's apparent movement across the sky.
- von Frisch had at last understood the honeybees' dance language and the world was forced to accept that another animal apart from ourselves — and a humble insect at that — could convey information in a symbolic fashion.

(a) Food source 40° to right of sun (b) Hive | Food source 180° (directly away) from sun Waggle run is made directly downwards on comb

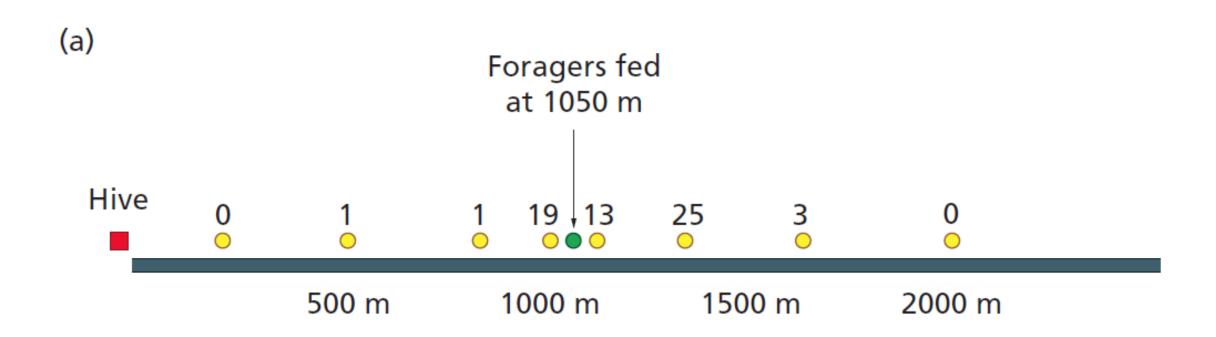
- (a) The dance is occasionally performed outside the hive on the horizontal entrance board; if so, the 'waggle' run of the dance points directly towards the food source.
- (b) When the dance is performed on the vertical comb inside the hive, the angle of the waggle run to the vertical is equal to the angle the sun makes with the food source.
- (c) Shows the honeybee's convention that directly downwards on the comb represents directly away from the sun. In the same way, upwards represents towards the sun.

 But do these dances actually communicate the information to other foragers in the hive?

Distance test:

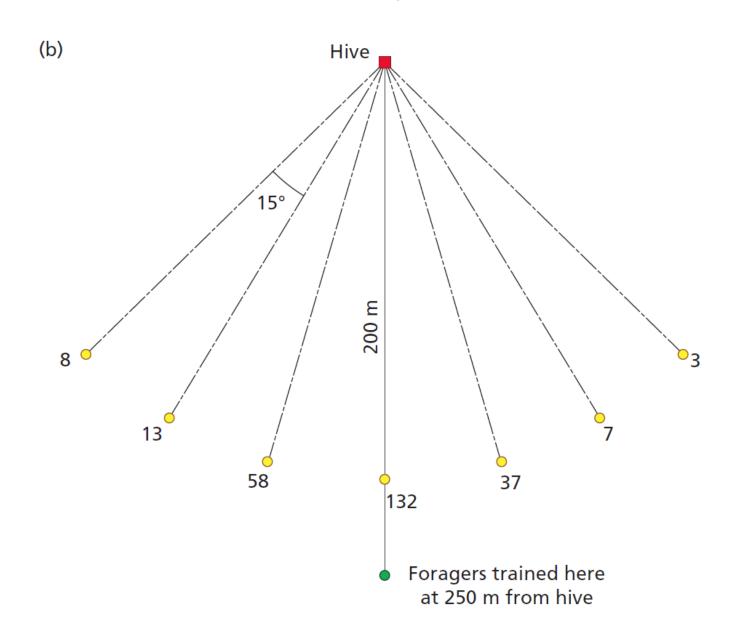
- Foragers were trained to a dish of dilute scented food 1050m east from the hive.
- Then a series of scented plates without food were put out at distances varying in the same direction from 100m to 2000m.
- Dancing was induced by suddenly increasing the sugar concentration at the feeding dish.
- Recruits were counted, but not captured, as they approached the different scent plates.
- The numbers above them record the number of visits made to each scent plate during the test.

Most recruits appeared at plates close to the feeding station.



Direction test:

- The procedure is much as for the distance test, but the scent plates are put in an array at the same distance but different directions from the hive.
- The majority of visits were made to dishes close to the bearing of the training station.



Watch video 2

https://www.youtube.com/watch?v=1MX2WN-7Xzc

- But how did such a complex behavior evolve?
- Can the extant bee species offer any clues?
- Apis florea is the only living bee species which dances a little differently than the other three. It dances on horizontal surfaces and simply points towards the direction of the food in its waggle dance.
- Other non-Apis bees provide hints at the evolution of this behavior.
- The possible first stage: Some stingless bees (e.g. *Trigona*) when returning from locating a food source, run about excitedly producing high-pitched buzzing sound. This excites the hive mates who smell the odour of the food on this forager and leave the nest searching for similar odors.
- The action of the dancing forager do not provide specific signals indicative of the direction or distance of the food.

- A possible intermediate stage: Some other *Trigona* species also convey information about the location of a food source.
- A worker that finds a food source deposits a pheromone on that source. As the bee returns to the hive she deposits pheromones along the path. When she returns to the hive she finds recruiters waiting who then seek out the source following this scent trail.
- A still more complex pattern: Other stingless bees, such as *Melipona*, convey separate distance and directional information.
- A dancing forager communicates information about distance by producing pulses of sound. The farther away the source, the longer the pulse.
- To transmit directional information, she leaves the nest with a number of followers and performs a short zigzag flight that is oriented toward the source of the nectar. The scout returns and repeats the flight a number of times before flying straight off to the nectar site, with the recruited bees in close pursuit.