Honey bee epidemiology and beekeeping practices: the example of American foulbrood

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HONEY BEE REPRODUCTION

Honey bees represent three types of reproduction:

• **Parthenogenesis**
  Drones are produced from unfertilized eggs

• **Sexual reproduction**
  Queens mate with 15-20 drones and store semen in the spermatheca for later fertilization of eggs

• **Vegetative reproduction**
  Number of colonies increase by colony fission (swarming)
When bees swarm, the queen and approximately half of the bees leave with the swarm.

The composition of the swarm represents almost a cross section of the bee population.
Swarming represents reproduction at the superorganism level.

If swarming bees carry pathogens, they are transferred to a new host colony.
Do superorganisms really exist!!??
SIMPLE NEURONS

THINKING BRAIN
DUMB BEES

SMART HIVE
HONEY BEE REPRODUCTION - CONSEQUENCES

- Colony level reproduction is imperative for survival of honey bees.

- There is a selective pressure on honey bees at colony level.

- This must be accounted for to understand the co-evolutionary processes of honey bees and their parasites.
KEY FACTORS IN EPIDEMIOLOGY

- Transmission
- Host population
- Parasite population
- Environment
KEY FACTORS IN EPIDEMIOLOGY

- Transmission

Horizontal transmission - between hosts within generation
  ex. flu virus

Vertical transmission - between hosts - between generation
  ex. transovarial transmission
KEY FACTORS IN EPIDEMIOLOGY

• **Horizontal** transmission

Horizontal transmission often dependent on host density
Horizontal transmission may expose the parasite to the environment
Horizontal transmission requires successful entry into host
  - Acquired/intrinsic immunity
  - Behavioural immunity
KEY FACTORS IN EPIDEMIOLOGY

• Vertical transmission

Vertical transmission independent of host density
Vertical transmission do not expose the parasite to the environment
Vertical transmission - parasite is already successfully established in the host
Acquired/intrinsic immunity often of less importance
Behavioural immunity does not influence parasite entry but may influence transmission (parasite manipulation vs host response)
Parasites using vertical transmission may not survive without an element of horizontal transmission
Horizontal vs vertical pathogen transmission:

- Pathogens transmitted mainly by horizontal routes will develop more virulent forms.

- Vertically transmitted pathogens will develop a more benign host/parasite relationship.

- There is always an important element of vertical parasite transmission in honey bees.
Within colony virulence vs colony level virulence

- Certain diseases have high virulence within colonies (i.e. kills infected individuals). In particular this is true for larval diseases

- Selection for high virulence within colonies will increase pathogen fitness only as long as it results in increased intercolony transmission
Horizontal vs vertical transmission:

• Thus, it is expected that disease in general should develop into benign infections in honey bee colonies.

• *Varroa* is not considered here because the host/parasite relation has not yet been moulded by evolution (and beekeepers prevent this from happening!)
Horizontal pathogen transmission:

Natural systems

- Drifting
- Robbing
- (infected nest sites)
Horizontal pathogen transmission:

Apiculture

- Transfer of bees and comb material
- Increased drifting
- Increased robbing
Vertical pathogen transmission:

- In natural systems during swarming
- In apiculture reduced - swarming control
Steps to increased parasite fitness in humans

Gain access → Transmission → Multiply
Steps to increased parasite fitness in honey bees

Gain access

Multiply

Transmission within colony

Transmission between colonies
Pathogen transmission routes in honey bees

Epidemiological implications of apiculture on disease transmission

• Apiculture greatly *increases* bee colony density leading to increased drifting/robbing. Apiculture also transfers bees, brood and comb material between colonies (*horizontal pathogen transmission*)

• Apiculture practices greatly *decreases*, or even prohibits swarming (*vertical pathogen transmission*)
Predictions - epidemiology

- Theory implies that apiculture *per se* selects for more virulent pathogens

- By killing colonies where pathogens manifest themselves through clinical symptoms, beekeepers may select for less virulent pathogens and balance the selection pressure imposed by apiculture
Conclusions - epidemiology

Honey bees reproduce at colony level by colony fission. This has important epidemiological consequences.

All pathogens in honey bees except one, where the host parasite relationship has been moulded by evolution, is probably primarily vertically transmitted and, thus, benign.

Apiculture alters the main mode of pathogen transmission from vertical to horizontal transmission. From this change, more virulent pathogens can be expected.

For further understanding of honey bee epidemiology horizontal and vertical transmission rates of pathogens must be studied.
AFB - infection

- Different strains of AFB vary in number of spores needed to produce infection

AFB - infection

- There are strains that kill the larva fast and strains that kill the larva slow

**AFB - infection**

- Larvae that die before capping is more readily removed by the bees, compared to larvae that die in sealed cells.

- Larvae that die earlier produce less spores.

- An apparent anomaly occurs in AFB, strains that are more virulent at colony level (fast killers) are less virulent at colony level (less likely to kill colonies).

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Lindström et al., 2010, in manuscript
AFB - horizontal transmission between colonies

Apiculture

Robbing

Drifting

Natural systems

(Robbing)

(Drifting)

Transfer of infected comb

Transfer of infected material

Feeding spore contaminated honey

Migrating infected colonies
AFB - horizontal transmission by robbing

- The importance of colony density for the transmission of AFB between honey bee colonies through robbing is documented
- Detectable spore transmission is not effective but does occur beyond 1 km
- A domino effect can be expected where apiary density is high

AFB - vertical transmission between colonies

Apiculture
(Swarming)

Natural systems
Swarming
Vertical transmission - mother colonies without symptoms


N=22
Vertical transmission - mother colonies with symptoms

Is AFB a highly contagious and colony level virulent disease!??

On the contrary! And the results are congruent with:

- Cases of AFB have never been found in honey bees south of the Sahara (Fries & Raina, 2003) until recently found in SA

- Nevertheless, AFB spores in honey have been found south of the Sahara (Hansen et al., 2003)

- Adult bees from wild colonies in areas without beekeeping rarely contain detectable spore levels (Hornitzky et al., 1996)

- Adult bees in swarms in areas with beekeeping are often contaminated by AFB spores (Hornitzky et al., 1996)

- Spore levels diminish over time in apiaries where clinically diseased colonies are removed from the site (Hornitzky, 1998).
Conclusions

It has been suggested that AFB is different from other bee diseases, being mainly horizontally transmitted and virulent at colony level (Fries & Camazine, 2001)

A pattern now emerges where this hypothesis must be refuted:

- AFB is not different from other bee diseases, it may be sustained in the host system through vertical transmission

- Differences in larval virulence of different strains of AFB may open for different transmission strategies (Genersch et al., 2005)

- All available data indicate that the problems with AFB in apiculture is induced by apiculturists
The extremely resilient spores of *P. larvae* could be needed for the pathogen because their fitness is independent of host survival (Day, 2002)

However, selection against virulence is also possible, if the death rate of the infected hosts is high compared with that of the propagules (Bonhoeffer et al, 1996).

The extremely resilient spores of *P. larvae* could be needed for the pathogen to:

- survive extended periods without brood where it replicates
- increase transmission probability if the host dies, without actually being dependent on host mortality at colony level for transmission between hosts
Thank you for your attention !!