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

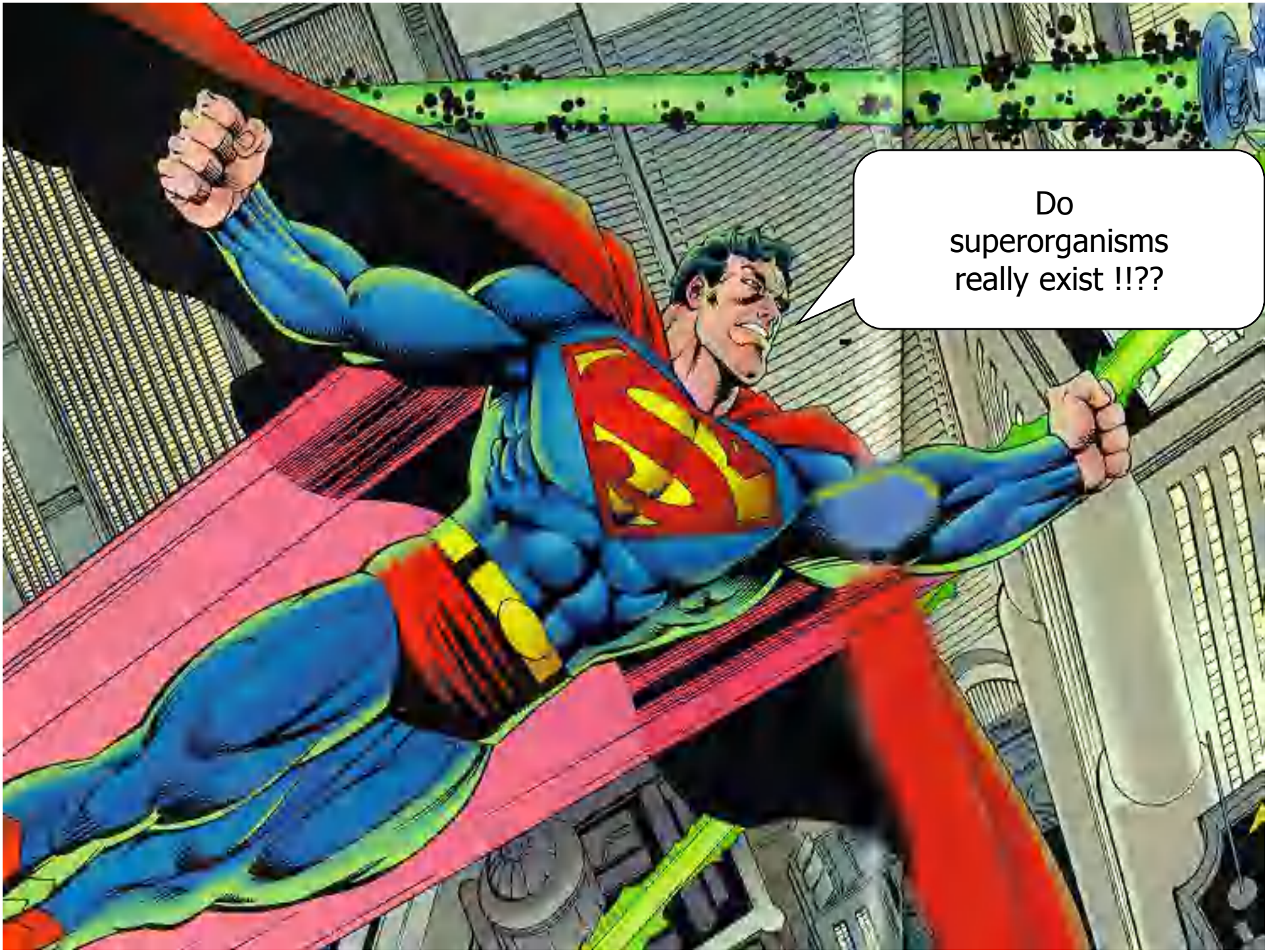
- Vegetative reproduction
  Number of colonies increase by colony fission (swarming)

When bees swarm, the queen and approximately half of the bees leave with the swarm

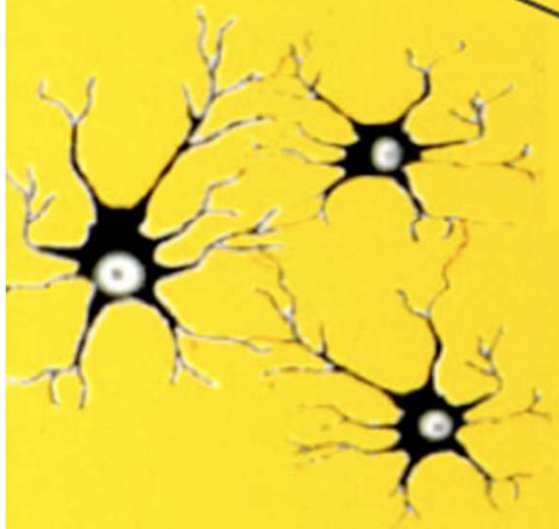
The composition of the swarm represents almost a cross section of the bee population

Swarming represents reproduction at the superorganism level

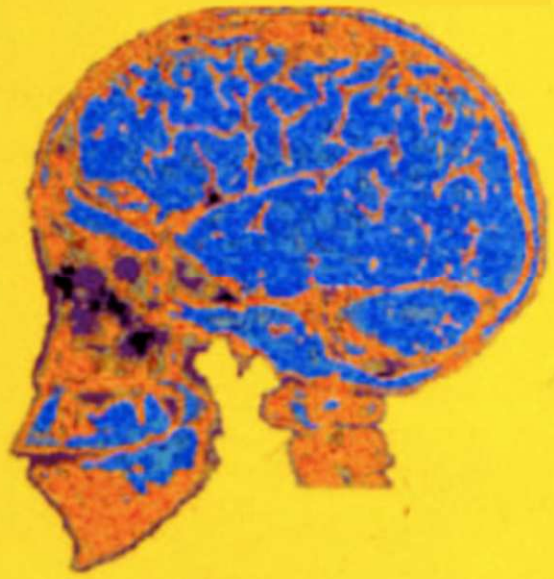
If swarming bees carry pathogens, they are transferred to a new host colony

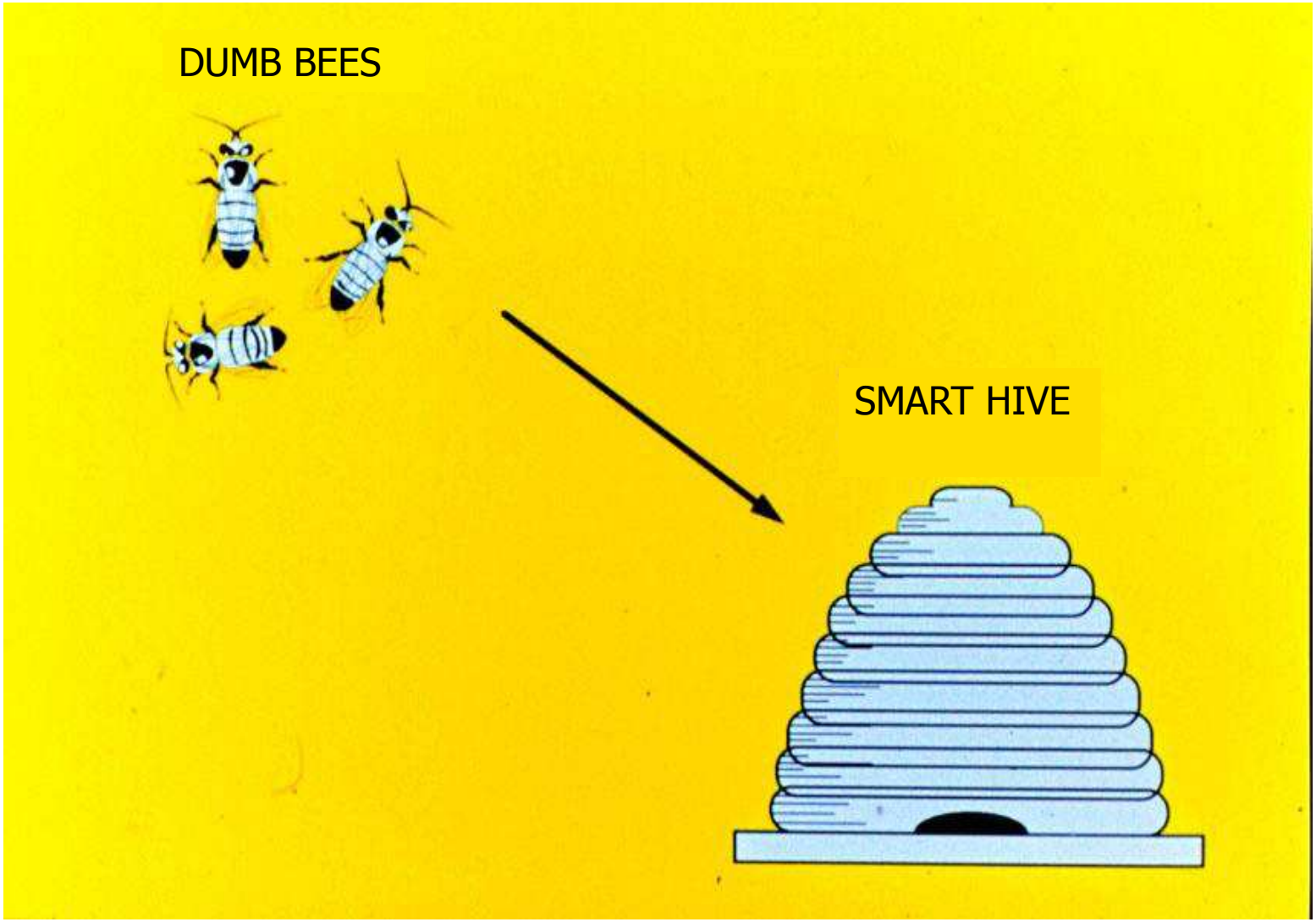

Do
superorganisms
really exist !!??

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 transmisson 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 transmisson - 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 respons)
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:

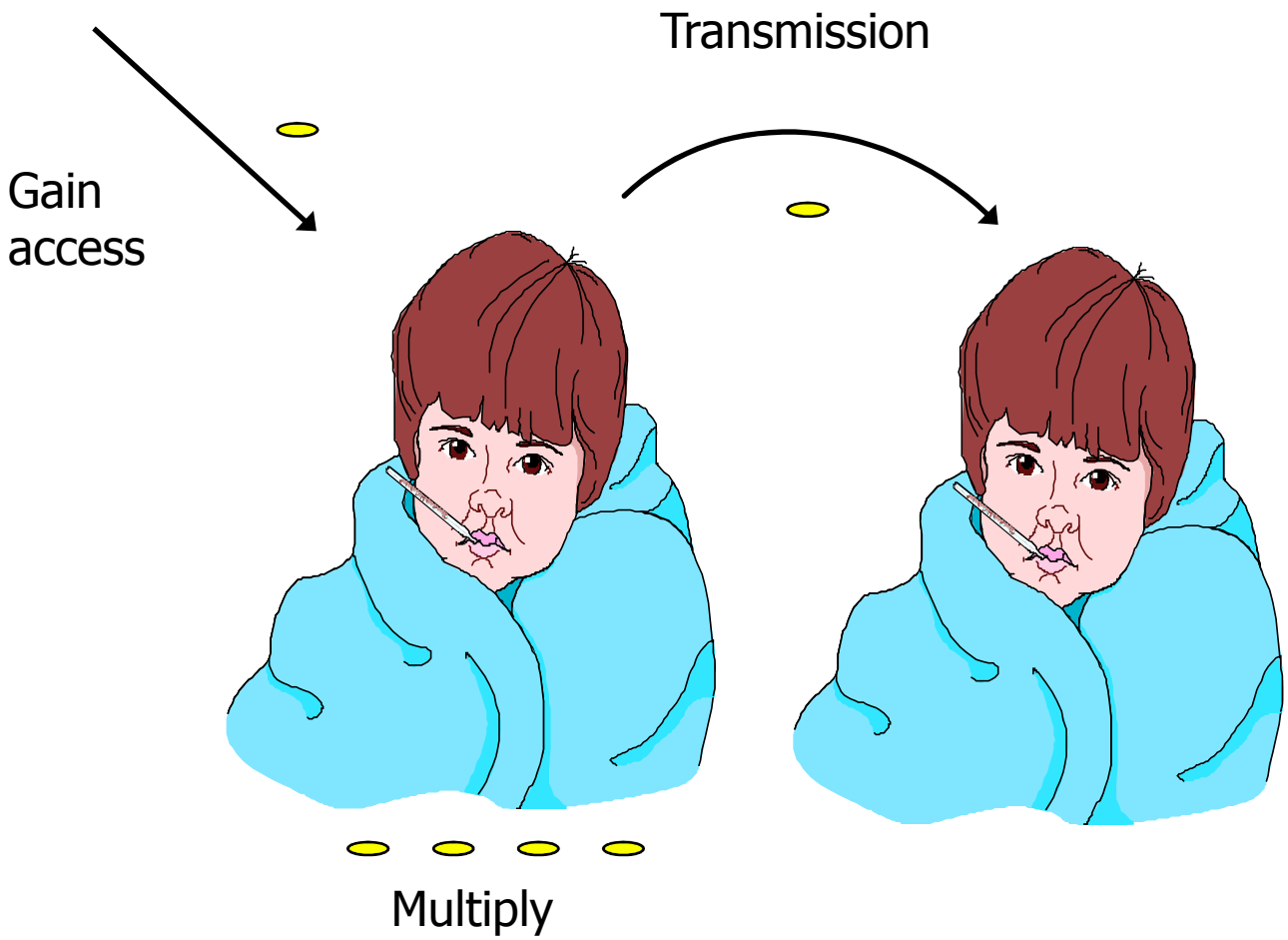
Apiculture

- Transfer of bees and comb material
- Increased drifting
- Increased robbing

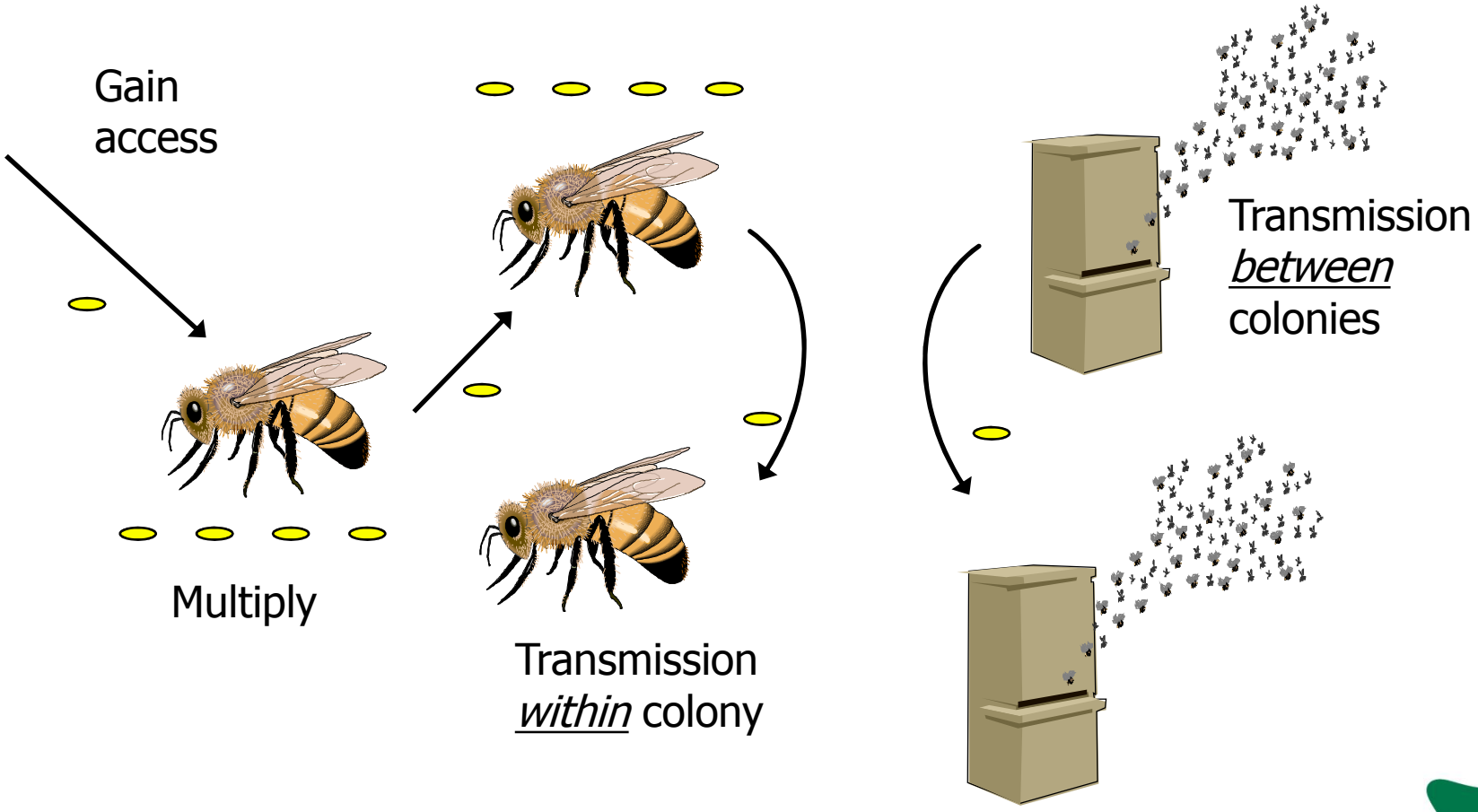
Vertical pathogen transmission:

- In natural systems during swarming
- In apiculture reduced - swarming control

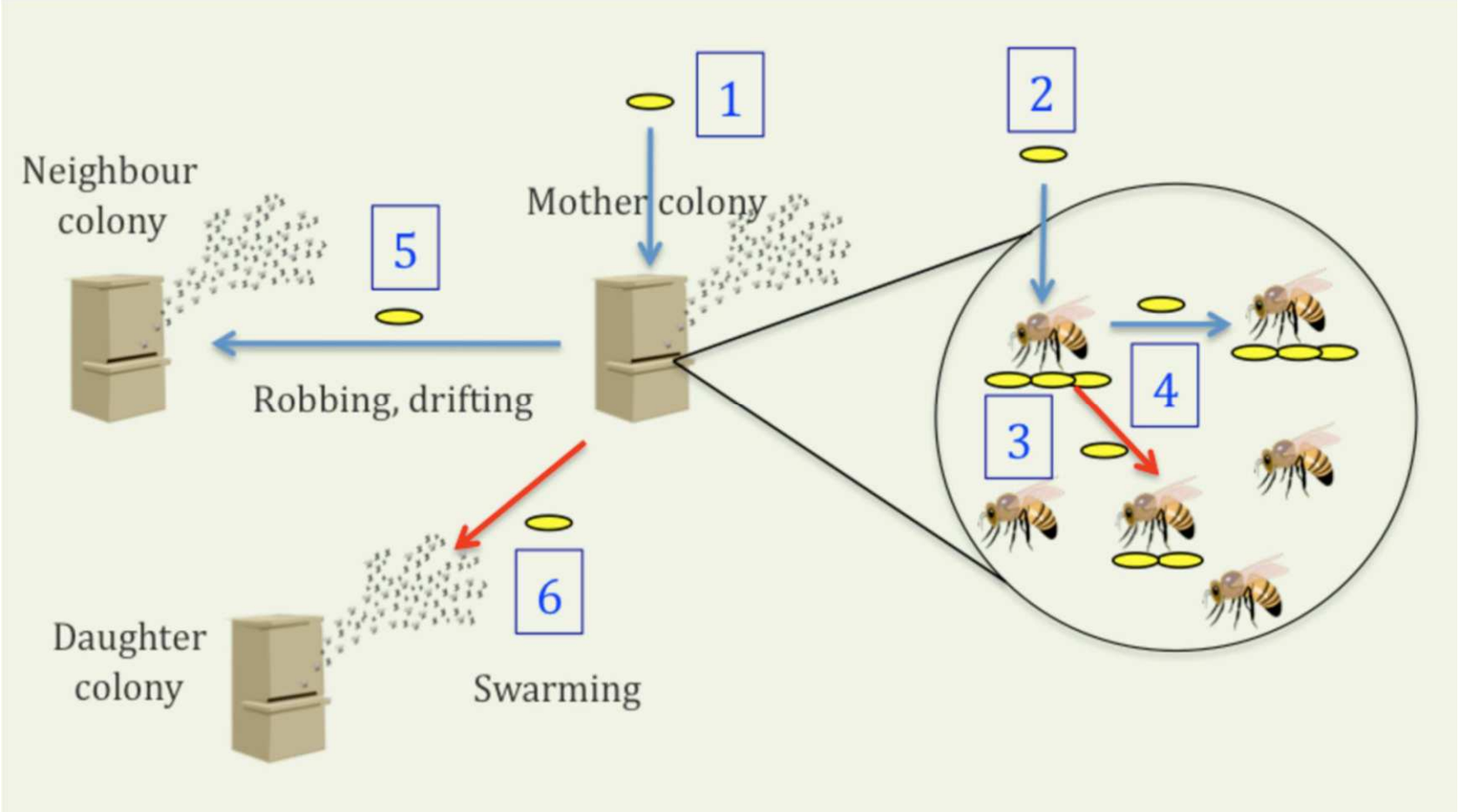
Steps to increased parasite fitness in humans



Steps to increased parasite fitness in honey bees



Pathogen transmission routes in honey bees



Fries, I., Genersch, E. Ashiralieva, A. 2011. Success of pathogens in insect societies: Epidemiology of American foulbrood (*Paenibacillus larvae*) in honey bee colonies. *Annual Review of Entomology*, in review.

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.

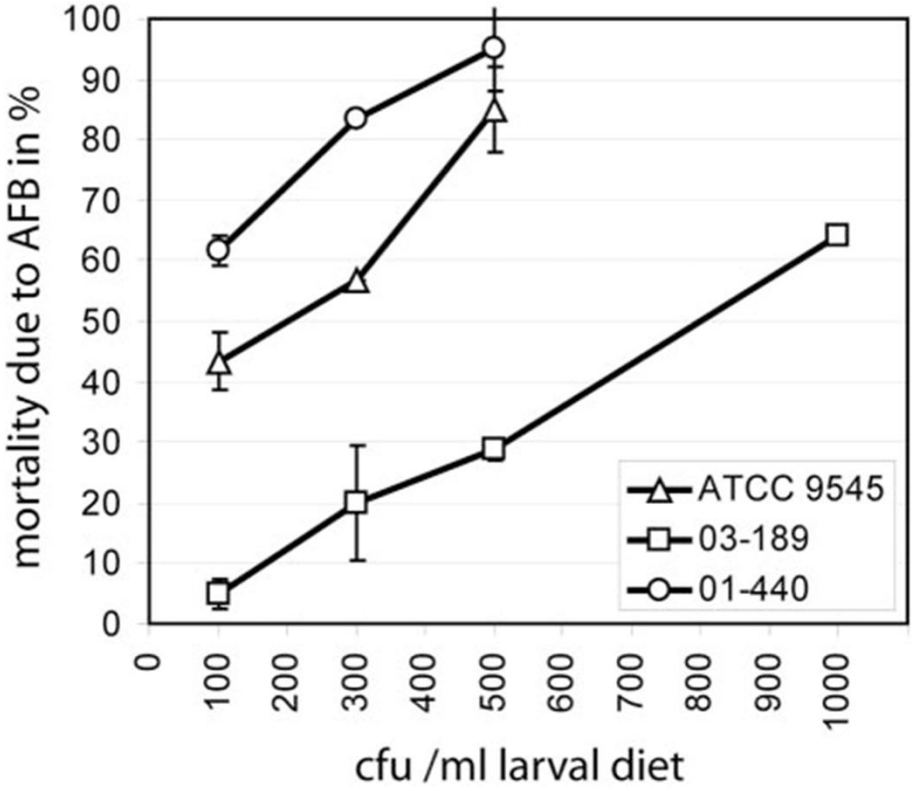
All pathogens in honey bees except one, where the host parasite relationship has been moulded by evolution, is probably primarily vertically transmitted and, thus, benign.

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



Genersch, E., Ashiralieva, A., Fries, I. 2005. Strain- and genotype-specific differences in virulence of *Paenibacillus larvae* subsp. *larvae*, a bacterial pathogen causing American foulbrood disease in honey bees. *Applied and Environmental Microbiology* 71, 7551-7555.

AFB - infection

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

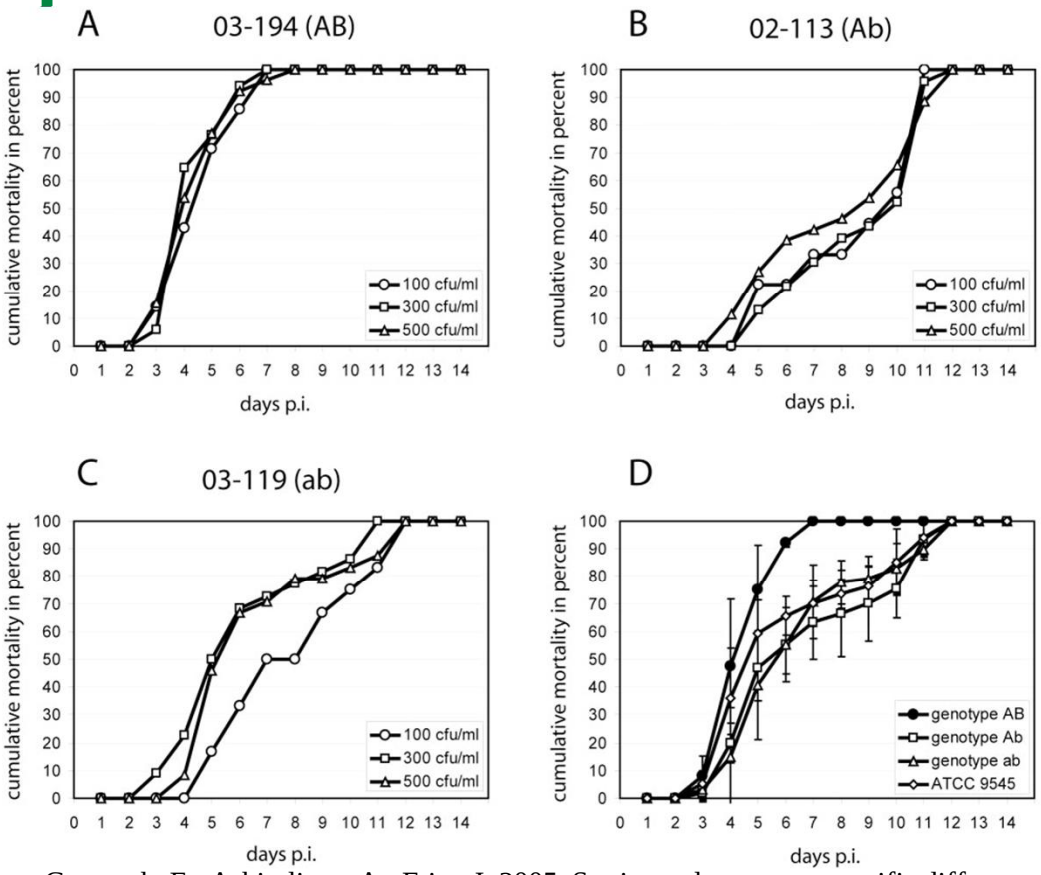


TABLE 2. *P. larvae* subsp. *larvae* genotype-specific LT_{100} and mortality after cell capping

P. larvae subsp. *larvae* genotype	LT_{100} (days p.i. [mean ± SD])	% Mortality after cell capping (mean ± SD)[a]
AB	7.8 ± 1.7	5.4 ± 3.2
Ab	11.2 ± 0.8	26.6 ± 7.3
ab	11.6 ± 0.6	20.2 ± 6.3
*a*β	11.3 ± 0.8	26.3 ± 2.8

[a] One hundred percent mortality is the total number of larvae that died from AFB.

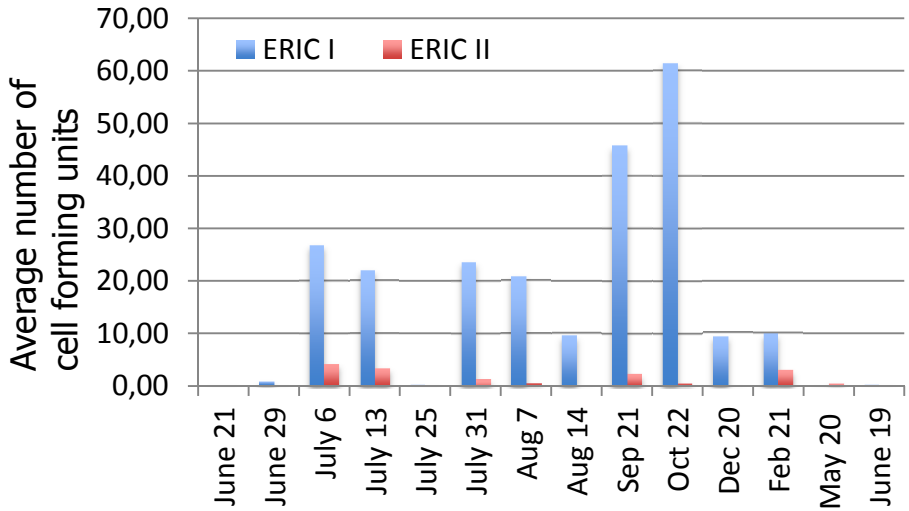
Genersch, E., Ashiralieva, A., Fries, I. 2005. Strain- and genotype-specific differences in virulence of *Paenibacillus larvae* subsp. *larvae*, a bacterial pathogen causing American foulbrood disease in honey bees. *Applied and Environmental Microbiology* 71, 7551-7555.

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)



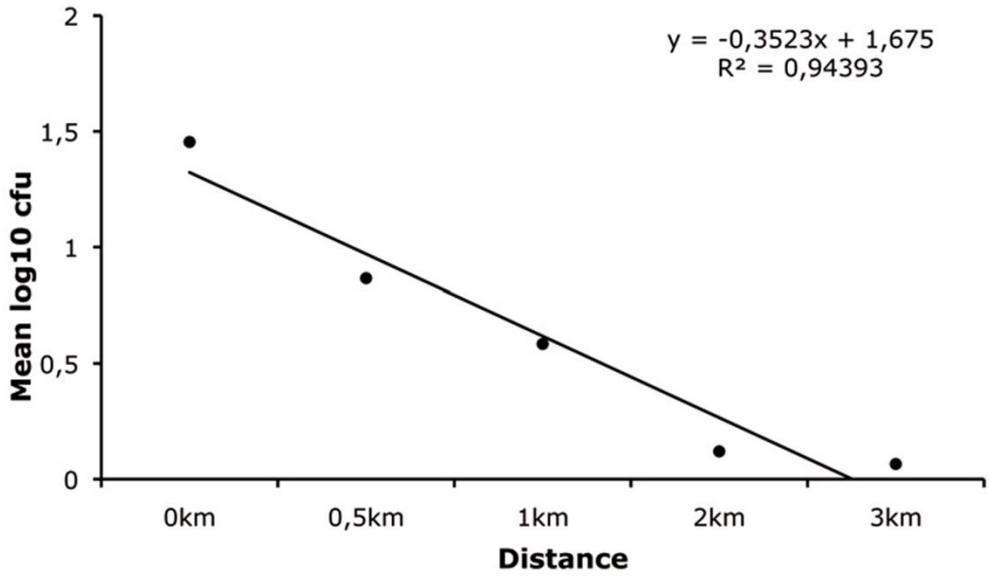
Lindström et al., 2010, in manuscript

AFB - horizontal transmission between colonies

Apiculture	Natural systems
Robbing	(Robbing)
Drifting	(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



Lindström, A., Korpela, S., Fries, I. 2008. Horizontal transmission of *Paenibacillus larvae* spores between honey bee (*Apis mellifera*) colonies through robbing. *Apidologie* 39, 515-521.

AFB - vertical transmission between colonies

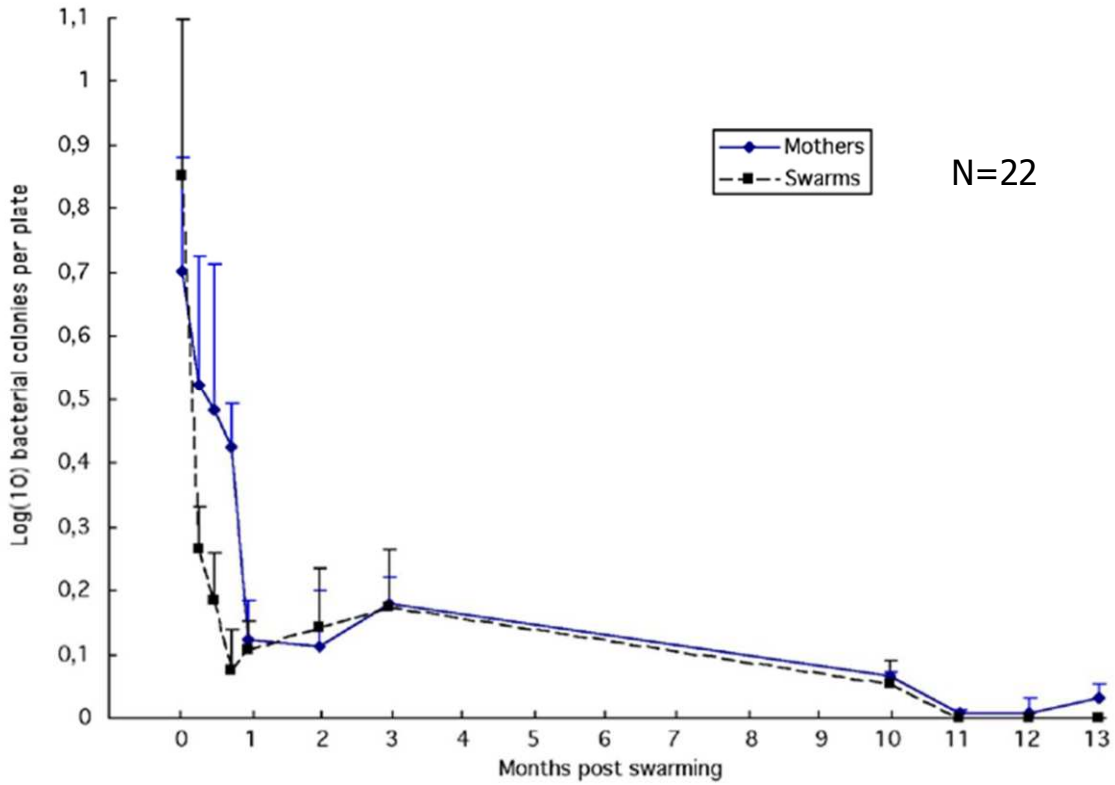
Apiculture

(Swarming)

Natural systems

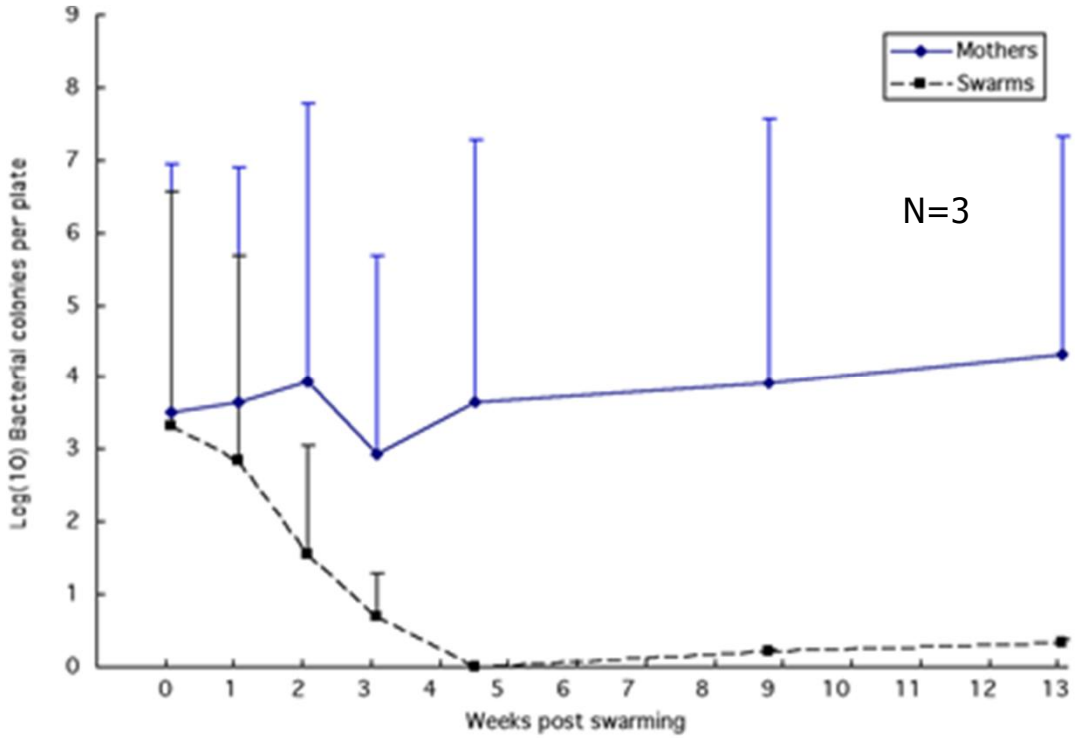
Swarming

Vertical transmission - mother colonies without symptoms



Fries, I., Lindström, A., Korpela, S. 2006. Vertical transmission of American foulbrood (*Paenibacillus larvae*) in honey bees (*Apis mellifera*). *Veterinary Microbiology* 114, 269-274.

Vertical transmission - mother colonies with symptoms



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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

Conclusions

Theoretical models have suggested that pathogens with resilient spores should evolve high virulence, 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
- to 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 !!