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Review article

Implications of horizontal and vertical pathogen transmission for honey bee epidemiology

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Abstract – The degree to which a disease evolves to be virulent depends, in part, on whether the pathogen is transmitted horizontally or vertically. Eusocial insect colonies present a special case since the fitness of the pathogen depends not only on the ability to infect and spread between individuals *within* a colony, but also on the ability to spread to new individuals in *other* colonies. In honey bees, intercolony transmission of pathogens occurs horizontally (by drifting or robbing) and vertically (through swarming). Vertical transmission is likely the most important route of pathogen infection of new colonies. Theory predicts that this should generally select for benign host-parasite relationships. Indeed, most honey bee diseases exhibit low virulence. The only major exception is American foulbrood (AFB). In light of current ideas in evolutionary epidemiology, we discuss the implications of horizontal and vertical pathogen transmission for virulence of AFB and other honey bee diseases.

honeybee / epidemiology / pathogen transmission / horizontal transmission / vertical transmission

1. INTRODUCTION

In the coevolution of hosts and their parasites, both the parasite and the host may gain in fitness by manipulating the behavior, physiology and life-history traits of one another (see, for example Hurd and Lane, 1998 and references therein). Parasites evolve specialized mechanisms for transmission either between individuals within a single generation (horizontal transmission), between individuals between one

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generation and the next (vertical transmission), or both, and these differences in mode of transmission greatly affect host fitness (Lipsitch et al., 1995a, b).

Here we discuss host-parasite relationships and modes of pathogen transmission in honey bees. We restrict our discussion to a social insect, the honey bee, because of our interest in examining the implications of host-parasite interactions in the special situation presented by sociality. We focus on honey bees because they are the most well-studied social insect, and because of the potential economic and applied implications of better understanding honey bee epidemiology.

Honey bee colonies consist of three castes; workers which number about 15000–50000, a few hundred drones and one reproducing female, the queen. A honey bee colony grows through the reproductive efforts of a single queen. In this haplodiploid system, fertilized eggs become non-reproductive workers who help raise their sisters, while unfertilized eggs become haploid male drones. Although the colony also may achieve some reproductive fitness through its drones, the production of new queens by workers and the subsequent division into two or several colonies, is fundamental for colony fitness (Moritz and Southwick, 1992). It is this reproductive swarming, which produces new colonies that makes honey bees a special case when discussing honey bee epidemiology and disease transmission.

2. DISEASE VIRULENCE AND PATHOGEN TRANSMISSION

Virulence can be defined as the degree to which parasitic infection decreases host survival and reproduction. Virulence is adaptive for the parasite only insofar as it promotes its own fitness, for example by promoting transmission of parasites to new hosts; often virulence is an unavoidable consequence of the parasite's reproduction. However, here is a trade off for the parasite. If the parasite's reproduction is too high, the infection may be so virulent that the host dies before sufficient numbers of propagules can be transmitted to new hosts. On the other hand, if parasite reproduction is too low, the parasite loses opportunities for transmission. The observed differences in parasite virulence in honey bees are more likely to be adaptions on the part of the parasites rather than counterdefenses on the part of the host, since parasites generally have much shorter generation time and higher mutation rates than their hosts. This enables the parasite to evolve faster than the host (Hafner et al., 1994). Nonetheless, it is often difficult to distinguish changes in parasite virulence from changes in host resistance to parasites (Schmid-Hempel, 1998).

A number of factors influence the evolution of virulence. The mode of disease transmission is one such factor believed to play a crucial role in molding pathogen virulence over evolutionary time (Lipsitch et al., 1996). The different modes of pathogen transmission can be divided into two categories: horizontal and vertical transmission. Horizontal transmission refers to parasite transmission between individuals of the same generation, while vertical transmission refers to that from parent to offspring (Canning, 1982). Compared with horizontal transmission, vertical parasite transmission is expected to select for decreased virulence. In this situation the goals of the host and parasite are aligned. Successful vertical transmission of a parasite requires that the host reproduces effectively, and thus the parasite reduces its own fitness if it adversely affects the overall health and reproductive capacity of its host. This idea has been tested experimentally and confirmed in a system using bacteria and bacteriophages transmitted either vertically or horizontally (Bull et al., 1991). Observations on fig wasps have also demonstrated a close correlation between nematode virulence and degree of horizontal transmission

relative to vertical transmission (Herre, 1993). Furthermore, experiments using 500 generations of a bacterial culture have also demonstrated a genetic trade-off between vertical and horizontal transmission of plasmids, although increased virulence due to horizontal transmission could not be demonstrated in this experiment (Turner et al., 1998). It should be noted that model simulations indicate that where both horizontal and vertical transmission occur, the expected virulence is not simply a function of which mode of transmission that predominates. Under some circumstances, increases in horizontal transmission may even decrease virulence (Lipsitch et al., 1995a). It is also clear that if parasites lower the fitness of the host, they will not survive unless there is also some degree of horizontal transmission (Lipsitch et al., 1995b). Clearly, the evolution of virulence in a pathogen depends on complex interactions between the host and the parasite; the trade-off between virulence and mode of transmission is but one important aspect.

Other factors have also been suggested to modulate virulence:

(1) Vectored vs. directly-transmitted pathogens. Vector-born pathogens are generally more virulent than directly-transmitted pathogens (Ewald, 1994). In general we would expect the adverse effects of high virulence on the host to diminish opportunities for parasite transmission to new hosts. However, this effect can be offset by the vector, if it promotes parasite transmission. (An example is malaria. Though this disease may incapacitate its host, the mobility of the mosquito vector provides ample opportunities for the malaria parasite to reach new hosts).

(2) Host density. Low host density favors low virulence whereas high host density favors high virulence (Bull, 1994). (High host density increases transmission opportunities and thus offsets the tendency for high virulence to lower transmission opportunities).

(3) Host longevity. In short-lived hosts, the parasite must “race against the clock” to assure transmission to a new host. In this situation, there is little disadvantage to the rapid development of large parasite populations (high virulence). In contrast, even when the parasite is not virulent, a long-lived host provides many opportunities for disease transmission (Lipsitch et al., 1996).

(4) Population structure. If there is sufficient structure in the host population, one generally expects to find decreased virulence in a horizontally-transmitted disease (Lipsitch et al., 1995a). Temporal or spatial structure of the host population that results in repeated or long-term contact with other members of the population increases opportunities for parasite transmission without increased virulence.

(5) Novel hosts. Pathogens introduced into a novel host population may be particularly virulent. This virulence may decrease over time as in the classic example of myxoma virus introduced to control rabbit populations in Australia. High virulence of the pathogen has been selected against because of the high host mortality (Fenner and Ratcliff, 1965).

(6) Pathogen replication rate. Increased replication rate increases host parasite load and is associated with high virulence. Within-host competition with other parasite strains may select for high replication rates, and high virulence even if this diminishes host survival and limits opportunities for pathogen transmission (May and Anderson, 1990).

(7) Life span of pathogen propagules. Virulence is favored in pathogens with long-lived propagules provided the host-parasite system is not in an equilibrium (Ewald, 1987). In particular, in parasites that have recently invaded a susceptible host population, greater propagule longevity may initially favour higher virulence; but once the equilibrium is reached the optimal virulence is independent of propagule longevity (Bonhoeffer et al., 1996).

The field of evolutionary epidemiology is rapidly expanding. A substantial number of theoretical papers have appeared in recent years attempting to provide a coherent framework for understanding the evolution of disease virulence and its relationship to factors such as the mode of parasite transmission, host density and host behavior. However, the perspectives provided by evolutionary epidemiology theories have only recently been applied to social insects. The analysis by Schmid-Hempel (1998) covers parasites in social insects in general, and has some discussion of honey bees. However, only a few experimental studies of social insects have direct bearing on evolutionary epidemiology and transmission of parasites, among them the studies of bumble bees (Schmid-Hempel and Loosli 1998, Schmid-Hempel and Schmid-Hempel 1993, see also Schmid-Hempel 1998).

Modes of pathogen transmission: horizontal and vertical

When considering colonies of social insects, we can subdivide horizontal and vertical transmission into both intracolony (between individuals within a colony) and intercolony (that between individuals from different colonies) components (Tab. I). For example, horizontal intracolony pathogen transmission most commonly occurs when an infected worker bee transmits a disease to another worker or a larva. Vertical intracolony transmission occurs when an infected queen transmits a pathogen to a daughter worker. However, from the point of view of parasite fitness, this form of vertical transmission is of no greater consequence than the horizontal worker to worker infections that occur with much greater frequency (due to the greater numbers of workers which interact with other workers in the colony, compared to the interactions between the solitary queen and her workers). (Note that we do not consider the other potential form of intracolony vertical transmission, transovarial infection, since this is not known to occur in honey bees.)

In the following section we discuss horizontal and vertical pathogen transmission in greater detail, and the relative importance of each of these modes of transmission for various honey bee diseases.

3. HONEY BEE SOCIETIES AND DISEASE TRANSMISSION

As a relatively homogeneous community of thousands of related individuals, one would expect a honey bee colony to be highly susceptible to rapid epidemic transmission of disease organisms. The high density of individuals within the colony, their close physical contact with one another (through casual contact, communication, and mutual grooming) and the trophallactic interchange of food and glandular substances all provide numerous and diverse opportunities for pathogen transmission.

Table I. Modes of pathogen transmission within and between honey bee colonies.

	Horizontal	Vertical
Intracolony	Worker to brood, worker, or drone Drone to worker or drone	Queen to daughter (worker) Queen to daughter (queen) Queen to son (drone)
Intercolony	Worker to worker or drone Drone to worker or drone (drifting, robbing)	Swarming

Furthermore the nest cavity, with its relatively constant temperature and moderate humidity, provides an ideal environment for pathogen growth and survival.

As a defense against pathogen transmission within honey bee colonies, we find that honey bee colonies possess a number of mechanisms that may have evolved specifically to curtail rampant spread of disease. These include:

(1) Use of antibacterial substances such as propolis to line the colony walls and seal the nest cavity;

(2) Antibiotic systems in pollen and honey stores;

(3) Hygienic cell cleaning behavior of the workers (reviewed in Boecking and Spivak, 1999);

(4) An undertaker caste of bees which removes dead, potentially diseased, carcasses (Visscher 1983);

(5) Grooming and allogrooming;

(6) Physiological mechanisms such as proventriculus that filters AFB spores, gut pH and immune mechanisms directed at preventing infection.

Although there are many characteristics that limit intracolony parasite transmission, few, if any, mechanisms have been described whereby honey bee colonies restrict transmission of parasites between colonies. The fact that foreign bees are rejected at the hive entrance during periods of dearth could be associated with defense against parasites, although this remains to be verified. Even so, foreign bees loaded with nectar are readily accepted during periods of food abundance (Jay, 1965; Pfeiffer and Crailsheim, 1998). This indicates that guarding as a mean of reducing parasite transmission is only partial, if it exists at all for this purpose.

From the disease organism's viewpoint, a honey bee pathogen must overcome three distinct fitness hurdles in order to reproduce and disperse to new hosts:

1. The pathogen must infect an individual (and usually must be able to multiply within this new host).

2. Generally, the pathogen must be able to infect additional individuals within the colony to assure a sufficient parasite load within the colony.

3. The pathogen must successfully gain access to new colonies.

In terms of fitness, the successful transfer of a pathogen's offspring to a new colony is a critical step in its life history. If a parasite or pathogen fails to achieve a foothold in another host colony, the parasite will not increase its reproductive fitness, regardless of how prolific it has been within the original host colony. Thus, hurdles #1 and #2 (intra-individual and intra-colony transmission) are important aspects of pathogen fitness only to the extent that they contribute to more efficient inter-colony transmission.

In contrast, a human parasite faces only the two first hurdles. Consider, for example, two intestinal parasites, the protozoan *Entamoeba histolytica*, infecting humans, and *Nosema apis*, a protozoan infecting the epithelial cells of the honey bee ventriculus. Both diseases are associated with similar symptoms of intestinal dysentery. *Entamoeba* assures its fitness by infecting and multiplying within its human host, and then using a fecal-oral route of transmission to infect new hosts. *Nosema* does the same, but is faced with the additional hurdle of gaining access to new colonies to assure its continued survival. It could be argued that humans also live in "colonies" (e.g. towns), and that the third hurdle discussed above applies also to humans. There may be some validity to this argument under circumstances where groups of humans are comparatively isolated. However, under normal circumstances, this is of minor importance, unlike the situation for honey bees in which the colony is the predominant unit of selection.

3.1. Horizontal intracolony disease transmission

Once a pathogen enters a colony or infects a bee, it may spread to other colony members. Such horizontal intracolony transmission is influenced by a variety of pathogen life-history characteristics. Some diseases affect only larval and pupal stages, and do not produce disease in adult bees. In such cases, adult bees (often the nurse bees which feed the brood) may act as mechanical vectors, carrying the disease to larvae. In other cases, the adult bees may become infected (but may show few or no symptoms) and spread the disease to brood (e.g. viruses) or other adults (e.g., nosema or amoeba disease where pathogens are transmitted through infected feces). Due to the confinement of the bee larvae to their natal cells, disease transmission between the larval stages of honey bees is restricted to infections where pathogens produce resting stages. When such resting stages are not sufficiently cleaned out from infected cells, the next larva to occupy the cell may become infected. Infection can also occur when bees are cleaning out cells and transmit infectious resting stages of the pathogens from one cell to another.

3.2. Horizontal intercolony transmission

Horizontal intercolony transmission of pathogens can occur through a number of routes. These include:

(1) Introduction of pathogens into a colony when an infected bee drifts from its own colony to another.

(2) Contact between individuals (or between individuals and infectious materials) during robbing. Robbing is an activity in which foraging bees from one colony invade another colony to steal honey.

(3) Contact between infected and uninfected individuals from different colonies during foraging.

(4) Contact with infectious material from the environment.

The drifting of bees into the wrong colony occurs frequently (Jay, 1965; Pfeiffer and Crailsheim, 1998) in apiaries where colony densities are greater than under natural conditions. In contrast, there is little or no evidence for disease transmission by drifting of individuals between feral colonies in the wild. In most cases, colonies are widely separated, precluding drifting of bees from one colony to another.

Robbing is a route of disease transmission that probably occurs at significant levels both under managed and natural conditions. However, bees generally rob only when there is little available foraging opportunities in the field, and they are only able to invade weak colonies. When outside food sources become scarce, guard bees in strong colonies usually detect and repel intruding bees from other colonies. On the other hand, when colonies become diseased and weakened, guarding becomes ineffective and robbing bees easily enter a sick colony where they may encounter pathogens. A robber bee brings pathogens back to its own nest on the surface of its body, or in robbed honey stored in its crop. An infected robber could also infect the visited colony with pathogens on its body, although this route of infection seems less likely.

Generally, bees are unlikely to become infected during contact with another bee during foraging. However, parasite transmission via flowers has been reported (Kevan et al., 1990) and may be of some importance for the transmission of spiroplasma (Clark, 1977).

There is the possibility that diseases such as chalkbrood and nosema may be spread indirectly from individual to individual through contaminated water or other inanimate materials. For example, the microsporidium *Nosema apis* can be acquired by individuals during collection of water contaminated by bee feces (L'Arrivée, 1965).

3.3. Vertical intercolony transmission

Vertical transmission of parasites occurs with the transfer of parasites between parents and their offspring, from one host generation to the next (Fine, 1975). In the case of social insect colonies such as honey bees, the most important form of vertical transmission of pathogens occurs during reproductive swarming, when the colony divides and propagules (swarms) bud off from the parent colony. These new swarms are typically headed by the old queen who leaves the original nest cavity to a daughter queen. In some cases a colony may produce several swarms at a time, and in this case, the additional (afterswarms) are headed by a virgin, yet unmated, queen. Intercolony vertical transmission is widespread, occuring whenever an infected colony swarms and brings with it infected individuals. Although some pathogens only affect brood, they can still be transmitted with adult bees. Thus, there is an element of vertical transmission involved in all honey bee diseases (see Tab. II).

3.4. Disease virulence and pathogen transmission in honey bees

Here, we focus on the issue of why certain honey bee diseases are more virulent

Table II. List of common honeybee pathogens, trivial names, mode of intercolony transmission and virulence. + or +++ under transmission indicates which mode of transmission that is estimated to be of most importance for molding the host-parasite relationship.

			Transmission		
Type of pathogen	Name of pathogen	Trivial name of disease/pathogen	Horizontal	Vertical	Virulence
Protozoa	*Nosema apis*	Nosema disease	+	+++	Benign
	Malphigamoeba mellificae	Amoeba disease	+	+++	Benign
Fungi	*Ascosphaera apis*	Chalkbrood	+	+++	Benign
	Aspergillus flavus	Stonebrood	+	+++	Benign
Bacteria	*Paenibacillus larvae larvae*	American foulbrood	+++	+	Lethal
	Melissococcus pluton	European foulbrood	+	+++	Benign
Virus	APV	Acute paralysis virus	+	+++	Benign*
	DWV	Deformed wing virus	+	+++	Benign*
Mites	*Acarapis woodi*	Tracheal mite	+	+++	Benign to lethal**
	*Varroa destructor***	Varroa mite	+	+++	Benign to lethal***

* Only severe effects when vectored by *Varroa* mites.
** Only severe where the mite has been recently introduced.
*** Only severe where the mite has been recently introduced or where effective mite control is employed.
**** New species described from *V. jacobsoni* (Anderson and Trueman, 2000).

than others, and how apicultural practices may affect disease virulence. We propose that the distinction between within-colony virulence and between-colony virulence will have an important effect on the evolution of pathogen virulence in honey bees.

Disease virulence and pathogen transmission in colonies of honey bees present a special case because host fitness depends upon the ability of the colony to produce swarms. In turn, parasite fitness depends not only on the ability to transmit propagules within the colony from one individual bee to another, but also on its ability to move from one colony to another, either vertically, through swarming, or horizontally, through bees and pathogens moving between colonies.

To understand honey bee epidemiology and disease virulence, one must distinguish between differences in pathogen transmission and virulence at both the individual and colony level. Among individual bees, certain bacterial, fungal and viral diseases have high intracolony virulence for larvae. In such cases, pathogens are transmitted to larvae (from nurse bees, or through brood cell contamination) and are highly virulent, rapidly killing the larva. In contrast, high intracolony virulence is almost unknown for adults. *N. apis* and *Malpighamoeba mellificae* can be picked up by adult bees from contaminated feces in the colony, but these parasites are not especially virulent, and only modestly shorten a bee's lifespan. In contrast, deformed wing virus (DWV) is a virulent disease that severely compromises adult survival since bees with deformed wings cannot fly, and are readily ejected from the colony by other workers. Other viral diseases also cause high adult mortality, but all these viral diseases are related to infestations with the parasitic mite, Varroa (*Varroa jacobsoni*, sensu lato) (Allen and Ball, 1996). Tracheal mite (*Acarapis woodi*) infestations can also result in high adult mortality, but this occurs only in overwintering bees (Gary et al., 1989). These cases of mite infestations are discussed separately below, since virulence in newly introduced parasites requires special considerations (Anderson and May, 1986).

At the colony level, we find that most diseases have low virulence. Whether this represents an adaptation of the parasite whose fitness interests are aligned with the host or an adaptive host response (or both) is difficult to determine. At the colony level, the only disease that has remained highly virulent for many years is American foulbrood (AFB). This unusual exception requires an explanation and is therefore discussed in detail below. The only other diseases that can be considered virulent at colony level are the newly introduced mite diseases (discussed in the section on case studies).

A pathogen may be virulent within the colony, rapidly killing individual larvae, but non-virulent at colony level. Chalkbrood, for example, is horizontally transmitted within the colony as adult bees carry spores that infect developing larvae. Once infected, the larvae quickly die. However, at the colony level, this pathogen is not virulent; colonies rarely, if ever, succumb to chalkbrood and although quantitative data is lacking, we believe infected colonies often swarm and produce new colonies that carry infectious spores on the swarming bees. In the competition between different strains of chalkbrood within colonies, the more virulent pathogen produces more propagules, and thus has the advantage. At the colony level, on the other hand, high within-colony virulence will be selected against if it impedes colony reproduction. The predicted outcome in this situation is a pathogen that is virulent within the colony but not virulent enough to keep colonies from swarming. When vertical transmission of pathogens can be accomplished effectively with *low* virulence, then strains using horizontal transmission and high virulence will be outcompeted (Lipsitch et al., 1996). Obviously, vertical transmission of pathogens

with low virulence can easily be achieved in honey bees as colonies divide during swarming. If vertical transmission requires *high* virulence, on the other hand, then strains of much higher virulence and horizontal transmission will be selected for (Lipsitch et al., 1996). This second scenario is, we believe, applicable to honey bees for one disease only – American foulbrood – with reasons for this developed later.

An element of vertical parasite transmission is always present in honey bee colonies, since bees increase in numbers by dividing the mother colony to produce daughter colonies. Since vertical transmission of parasites favors development of a benevolent host-parasite relationship, highly virulent parasites are unlikely to evolve in honey bees. Actually, swarming is likely to be advantageous for both the colony (since it reduces the parasite load within the colony) and for the parasite (since it provides a mechanism of disease transmission to new colonies). This regulatory effect of swarming has been proposed for honey bee tracheal mites (Royce et al., 1991). Furthermore, evolution will likely favor vertical transmission since it provides a safe route of transmission for pathogens. The parasites can transfer from mother colonies to daughter colonies, without ever leaving their hosts and facing exposure to the hazards of a hostile environment.

Table II summarizes the mode of transmission and pathogenicity at the colony level for a number of important honey bee pathogens. In Table II we find only three pathogens that commonly result in colony mortality: American foulbrood, tracheal mites, and Varroa mites. We discuss these diseases in detail in the next section.

3.5. Case studies

3.5.1. Mite diseases

Tracheal mites were reported in central Europe in the early part of this century (Rennie et al., 1921). When first discovered they apparently caused considerable colony losses, these mites are now considered a benign disease, and do not require control by beekeepers (Ruttner, 1971). In Finland, where the mite was recently introduced, it is spreading and causing considerable colony losses (Korpela, 1998). In North America, the tracheal mite was first found in 1984 (Delfinado-Baker, 1984) and caused massive colony losses (Scott-Dupree and Otis, 1990). Following the initial devastating effects from the tracheal mite infestations, the dramatic impact of the parasite seems to have diminished and we expect this development to continue. The hypothesis that the mode of transmission molds pathogen virulence predicts that a parasite such as the tracheal mite will be transmitted horizontally between colonies during the initial phase before the infestation is well established. Later, the vertical spread will be the main source of transfer to new colonies as the parasite has become widespread. Over time, the most susceptible colonies die and the selective pressure on the parasite will select against effects on colonies that inhibit reproductive swarming. Thus, a benign host parasite relationship should evolve.

In the case of Varroa, which is a worldwide menace to beekeeping, we believe apicultural practices are responsible for maintaining virulent forms of the pathogen. In areas where the parasite has been established for several decades in honey bee populations, without being controlled by beekeepers, the parasite no longer is lethal to infested colonies. This is the case in South America both for Africanized bees and bees of European origin (Rosenkranz, 1999) as well as in North Africa (Ritter, 1990). The mechanisms for Varroa mite tolerance seem to be different among different sub-populations of honey bees and probably developed independently (Rosenkranz, 1999). Note, however, that the precise nature of the honey bee-Varroa host parasite relationship is complicated by the fact that this parasite is not one species, but a species complex

(Anderson and Fuchs, 1998), with the mite infesting European bees recently redescribed as *Varroa destructor* (Anderson and Trueman, 2000). Under the influence of apicultural management practices that promote opportunities for horizontal transmission, a more virulent host-parasite relationship should be retained. With a long history of co-adaptation on its natural host (the Asian honey bee, *Apis cerana),* the Varroa mite is in fact a benign parasite, as expected for a pathogen that is primarily vertically transmitted. The European and Asian honey bees have very similar life histories and it seems likely that Varroa should develop a benign host parasite relation in European honey bees, if given the opportunity.

3.5.2. American foulbrood

American foulbrood (AFB) (caused by the spore-forming bacterium *Paenibacillus larvae larvae*) regularly kills honey bee colonies under natural conditions. The disease is often insidious, with symptoms discovered by the beekeeper only late in the disease process (Hansen and Brødsgaard, 1999; Ratnieks, 1992). Although some colonies are resistant to the disease, susceptible colonies succumb to the infection.

What is unusual about this parasite's life history that could promote a virulent, lethal infection? Under natural conditions, the disease readily spreads horizontally when weakened, infected colonies are robbed by bees from other colonies, or when new swarms occupy nestsites where the former colony has succumbed to AFB. In general, horizontally transmitted parasites are expected to modulate their virulence to strike a balance between their own reproduction and host mortality (Anderson and May, 1982). If host mortality increases pathogen transmission between hosts, virulent forms of the pathogen will be selected for. A major difference between AFB and other honey bee diseases is the presence of a long-lived spore that can retain its viability for decades under diverse environmental conditions (Shimanuki and Knox, 1994). Spore viability allows the pathogen to "wait" long periods and still be assured of eventual transmission to new colonies. Even when a colony dies, there is ample opportunity for transmission of the bacteria to new colonies. This would not be the case for other bacteria, viruses or protozoal pathogens that do not form such durable spores.

Spore forming pathogens like *P. larvae larvae*, are effectively spread by robbing bees (Ratnieks, 1992). Robbing occurs commonly in apiaries. It also occurs among widely separated feral colonies since bees can readily use olfactory cues to locate distant hives. There is no evidence that colonies avoid robbing disease-infected hives, and infected nest sites are not avoided when new nests are established (Ratnieks and Nowakowski, 1989).

In addition to pathogen spread through robbing or the occupation by swarms of infected sites, there is the potential for horizontal spread of AFB by drifting bees. However, this route is probably of minor importance even in commercial beekeeping where colony density may be extremely high (Goodwin et al., 1994), and even less so under natural conditions where low colony density hinders intercolony drifting. Likewise, there is the possibility of spores being carried by adult bees during swarming, although this is unlikely to result in clinically diseased colonies. From feeding experiments, we know that very high spore levels must be fed to colonies to produce clinical symptoms of AFB (Hansen et al., 1988). Large numbers of spores need to be in the colony to produce infection, although individual young larvae may succumb to disease from low spore doses (Hoage and Rothenbuhler, 1966). Only strong colonies produce daughter colonies and as colonies are weakened by AFB, they will be less likely to swarm, thus lowering the opportunity for vertical parasite transmission. Beekeeping practices to control AFB provide further evidence that vertical pathogen

transmission during swarming is of minor importance for this disease. To cure foulbrood-infected colonies, beekeepers shake the adult bees off the old diseased combs and force them to build new combs (Hansen and Brødsgaard, 1999). This treatment is similar to natural swarming since the swarm constructs new comb as it establishes the colony.

The life-history strategy of AFB is probably the result of a selection pressure in which the comparatively high rate of horizontal transmission compared to the low level of vertical transmission favors the development of a relatively aggressive parasite. The opportunity for horizontal transmission could be important in explaining why AFB is the only lethal honey bee disease where the host parasite relationship has been molded over evolutionary times. The extremely stable spores produced by *P. larvae larvae* adds a further selective advantage for the pathogen since weakened or killed host colonies can still serve as sources of disease transmission between colonies.

4. EPIDEMIOLOGICAL IMPLICATIONS OF APICULTURAL PRACTICES FOR THE TRANSMISSION OF BEE DISEASES

4.1. Effects of apicultural practices

Beekeeping practices can have important epidemiological consequences. Under natural conditions honey bees are restricted to natural cavities, such as hollow trees and colony density is low. In most parts of the world, the vast majority of bee colonies are kept and managed by beekeepers. Housing for colonies is supplied by the beekeeper and the density of colonies is much higher than in nature. Standard beekeeping practices, which include swarm control and apiaries with large numbers of colonies, will inevitably increase the horizontal transmission and decrease the vertical transmission of pathogens. We predict that this is likely to have an impact on the development of pathogen virulence since apicultural practices alter the probability for horizontal versus vertical transmission of pathogens.

Apicultural practices increase the risk of drifting of infected bees between colonies. Not only do drones frequently enter foreign colonies (Free, 1958), but substantial drifting also occurs of workers (Jay, 1965; Pfeiffer and Crailsheim, 1998). Management of colonies during periods of nectar shortage and feeding of colonies often induces robbing behavior, which again may transfer infected bees or infected food stores between colonies. Besides these increased risks for horizontal pathogen transmission, high bee densities also result in resource competition between colonies for pollen and nectar, which may reduce overall colony fitness (Bailey and Ball, 1991). Furthermore, managing colonies to increase production often involves shifting of comb (brood combs as well as other comb) between colonies. This greatly increases the probability of horizontal transmission of all types of pathogen that may be transmitted by contaminated wax, such as nosema (Bailey, 1953), AFB (Ratnieks, 1992) or chalkbrood (Koenig, 1987). Managing colonies also involves moving bees between colonies (for example to strengthen weak colonies). This also facilitates horizontal transfer of disease agents on or in adult bees.

As described earlier, honey bee colonies possess a variety of mechanisms to limit disease transfer within the colony, but these systems may be overwhelmed by certain beekeeping practices that affect intracolony transmission. When bees are crushed during hive manipulations, pathogens may spread in the colony as bees clean out the dead remains. Similarly, disease may be transmitted through feeders when bees defecate in the food. Hive manipulations that induce defecation of bees inside the hive may also promote disease transmission. Furthermore, colony splits or other hive manipulations may alter the age structure of the

bees and disturb the natural task distribution among workers. This can affect hygienic behavior performance, important for controlling AFB and other brood diseases (Spivak and Gilliam, 1999a, b).

Among horizontally transmitted diseases, the evolution of pathogen virulence is also affected by host density: high host densities favor higher virulence (Bull, 1994). The rationale is that with high host densities, the pathogen can more easily reach new hosts, and offset the fitness disadvantages to the host that occur with highly virulent pathogens. In contrast to apicultural conditions, the normal situation is for bee colonies to be widely scattered at low densities. Honey bees are long-lived under favorable conditions. Provided the pathogen is not highly virulent, this affords continued opportunities for horizontal pathogen transmission between colonies even when they are widely scattered. Thus, even if the trade-off between vertical and horizontal pathogen transmission is not considered, lower virulence is expected for horizontally transmitted pathogens in honey bees under natural conditions compared to conditions created by apiculture.

Honey bees swarm to reproduce. Swarming behavior results in vertical pathogen transmission. Since bees that swarm produce less honey, beekeepers generally restrict swarming through a variety of management practices. To increase the number of colonies or to replace losses, beekeepers make nuclei from old colonies. Normally these nuclei receive a developing queen cell or a mated queen from pre-selected stock and, thus, prevent the formation of daughter colonies genetically related to the colonies from which nuclei were formed. In this system, pathogens may be transferred to daughter colonies on adult bees and with brood combs. However, this is not equivalent to vertical pathogen transmission since daughter colonies will, for the most part, be unrelated to the colonies from which they were formed. On the contrary, from a selective perspective forming of new colonies under managed conditions will promote horizontal transmission of pathogens to new colonies rather than the vertical transmission that occurs under natural swarming conditions.

4.2. Changes in management practices that would be expected to diminish disease virulence and transmission

Modern evolutionary epidemiology suggests that behavioral practices can greatly affect the future course and virulence of disease (Ewald, 1994). Undoubtedly, apiculture creates numerous conditions where horizontal pathogen transmission is favored over vertical transmission. Thus, theory suggests that apiculture per se will select for more virulent honey bee pathogens. As a consequence, beekeepers could benefit if they instituted simple practices that reduce horizontal transmission. For example, the size of apiaries can be limited, and colonies can be placed to minimize drifting. Furthermore, the transfer of bees and brood between colonies should be limited as should all practices that increase the risks for within hive defecation of bees or crushing of bees. Considering vertical pathogen transmission, it is impractical to suggest that colonies should be allowed to swarm to favor this mode of transmission. However, a similar effect may be accomplished by paying attention to pathogen impact when breeding stock is selected. Beekeepers should continually select strains of bees that show disease resistance.

What we describe are good beekeeping practices. The evolutionary perspective on transmission of pathogens simply adds another dimension to old arguments about the management of bees, and suggests that more severe disease problems can be expected to develop unless good beekeeping practices are maintained. The predictions presented in this paper align modern evolutionary epidemiology with honey bee

pathology. The practical implications of this perspective still remain to be verified in field experiments.

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Résumé – Implications, pour l'épidémiologie de l'abeille domestique, de la transmission horizontale et verticale des agents pathogènes. Des discussions récentes sur l'épidémiologie des maladies suggèrent que la distinction entre transmission horizontale et transmission verticale d'un agent pathogène joue un rôle crucial dans la compréhension de la formation de la virulence d'une maladie au cours de l'évolution. Comparée à la transmission horizontale, la transmission verticale est plus susceptible de sélectionner une relation hôte-parasite bénigne qu'une virulente.

La transmission et la virulence des agents pathogènes chez les colonies eusociales d'insectes, telles que les abeilles, présente un cas particulier car la vitalité d'un agent pathogène dépend non seulement de sa capacité à infecter et à se répandre parmi les individus de la colonie, mais aussi de sa capacité à se répandre d'une colonie à l'autre. Chez les abeilles, une telle transmission inter-colonies peut se faire soit horizontalement (par exemple par la dérive d'abeilles d'une colonie à une autre ou par des abeilles pénétrant temporairement dans d'autres colonies pour dérober du miel), soit verticalement (lorsque la colonie se reproduit par essaimage). Contrairement aux conditions d'exploitation dans les ruchers, où la dérive et le pillage ont lieu fréquemment en raison des fortes densités de population, en conditions naturelles les colonies sont beaucoup plus espacées et la transmission verticale est la voie principale pour l'infection de nouvelles colonies. Selon la théorie de l'épidémiologie de l'évolution, cela devrait généralement sélectionner des relations hôte-parasite bénignes. Pourtant, la transmission inter-colonies des agents pathogènes de l'abeille se fait principalement verticalement par l'essaimage et ces maladies présentent une virulence comparativement faible. La seule grande exception est la loque américaine (AFB), causée par la bactérie *Paenibacillus larvae larvae*. Les spores de l'AFB restent viables durant des décennies et, une fois établie, l'infection est très virulente et conduit facilement à la mort des colonies infectées. Elle se transmet facilement horizontalement aux autres colonies et *P. larvae larvae* est probablement le seul agent pathogène de l'abeille pour lequel la transmission horizontale de la maladie domine.

Sans aucun doute, l'apiculture crée des conditions dans lesquelles la transmission horizontale est favorisée aux dépens de la transmission verticale. Ainsi la théorie suggère que l'apiculture en soi sélectionne les agents pathogènes les plus virulents. En conséquence les apiculteurs pourraient gagner à réduire la transmission horizontale en limitant la taille des ruchers et en disposant les colonies de façon à restreindre au minimum la dérive. En outre, le transfert des abeilles et du couvain d'une colonie à l'autre devrait également être réduit au minimum de même que toutes les pratiques qui augmentent les risques d'écrasement d'abeilles ou de défécation des abeilles à l'intérieur de la colonie.

En ce qui concerne la transmission verticale, il est peu réaliste de suggérer de laisser essaimer les colonies pour favoriser ce mode de transmission. Pourtant on pourrait obtenir un effet analogue en prêtant attention aux maladies lors de la sélection des colonies éleveuses. Les agents pathogènes qui se manifestent par des symptômes seront défavorisés si les apiculteurs ne produisent de nouvelles colonies qu'à partir de colonies indemnes des symptômes cliniques.

Nous décrivons ici de bonnes pratiques apicoles. Mais l'introduction en apiculture

d'une perspective évolutionniste sur la transmission des agents pathogènes ajoute une autre dimension aux vieux arguments et suggère que des problèmes pathologiques plus sérieux vont progressivement voir le jour, à moins que de bonnes pratiques apicoles ne soient maintenues. Les prévisions présentées dans cet article s'alignent sur l'épidémiologie de l'évolution et la pathologie de l'abeille. Il reste à vérifier dans des expériences de terrain les implications pratiques de cette perspective.

***Apis mellifera*/ épidémiologie / transmission agent pathogène / transmission horizontale / transmission verticale**

Zusammenfassung – Bedeutung horizontaler und vertikaler Verbreitung von Pathogenen für die Entwicklung von Krankheiten der Honigbienen. Die neueren Erörterungen der Entwicklung von Krankheiten legen nahe, dass die Unterscheidung zwischen horizontaler und vertikaler Ausbreitung eines Pathogens einen wesentlichen Schlüssel zum Verständnis der Ausformung der Virulenz einer Krankheit in evolutiven Zeiträumen bietet. Vertikale Verbreitung führt wesentlich wahrscheinlicher zur Entwicklung gutartiger Wirt-Parasitbeziehungen als horizontale Verbreitung. Die Übertragung und Virulenz von Krankheitserregern bei sozialen Insekten wie Honigbienen stellt einen besonderen Fall dar, da die Lebensfähigkeit eines Parasiten nicht nur von der Verbreitung zwischen den Individuen innerhalb der Völker abhängt, sondern ebenso von der Fähigkeit der Verbreitung zwischen Völkern. Bei Honigbienen kann eine solche Verbreitung ebenfalls horizontal geschehen (etwa durch Verflug von Arbeiterinnen zwischen Völkern oder durch kurzzeitiges Eindringen um Honig zu stehlen) oder aber vertikal, wenn sich die Völker durch Schwärme vermehren. Im Gegensatz zu bewirtschafteten Völkern (bei denen Verflug oder Räuberei wegen der hohen Völkerdichte häufig sind) ist unter natürlichen Verhältnissen die vertikale Verbreitung durch den hohen Abstand zwischen den Völkern der hauptsächliche Weg, auf dem pathogene neue Völker befallen. Die evolutionäre epidemiologische Theorie führt zu der Voraussage, dass dies generell eine Selektion in Richtung eher gutartiger Wirt-Parasitbeziehungen führen sollte.

In der Tat werden Krankheitserreger überwiegend vertikal über die Schwarmbildung weitergegeben, und diese Bienenkrankheiten sind von vergleichsweise geringer Virulenz. Die einzige größere Ausnahme bildet die durch das Bakterium *Paenibacillus larvae larvae* hervorgerufene Amerikanische Faulbrut (AFB). AFB-Sporen können über Jahrzehnte überleben, einmal erfolgte Infektionen sind hochvirulent und können befallene Völker leicht zugrunde richten. Die Krankheit wird leicht von Volk zu Volk übertragen und ist wahrscheinlich die einzige Bienenkrankheit, bei der der horizontale Übertragungsweg dominiert.

Ohne Zweifel schafft die Bienenhaltung Bedingungen, durch die die horizontale Übertragung gegenüber der vertikalen Übertragung begünstigt wird. Die Theorie weist darauf hin, dass Bienenhaltung an sich geeignet ist, Bienenkrankheiten mit höherer Virulenz herauszuselektieren. Als Schlussfolgerung hieraus könnte die Bienenhaltung daraus Nutzen ziehen, die horizontale Weitergabe von Krankheiten durch geringere Größe der Bienenstände und verflugsmindernde Aufstellung der Völker zu verringern. Weiterhin sollte der Austausch von Bienen und Brut zwischen Völkern sowie alle Vorgehensweisen vermieden werden, die das Abkoten in den Völkern oder das Zerdrücken von Bienen hervorrufen.

In Betrachtung vertikaler Weitergabe ist es praxisfern, zu verlangen, dass den Völkern das Schwärmen ermöglicht werden sollte um diesen Übertragungsweg zu begünstigen. Allerdings könnte ein ähnlicher Effekt erreicht werden, wenn bei der Selektion von Zuchtvölkern auf Krankheiten geachtet wird. Krankheitserreger, die symptomatische Effekte hervorrufen werden benachteiligt,

wenn die Bienenhalter neue Völker nur aus von klinischen Symptomen freien Völkern erzeugen.

Was wir beschreiben ist gute Bienenhaltungspraxis. Allerdings wird durch die evolutionäre Perspektive auf die Rolle der Übertragungswege von Krankheiten eine neue Dimension zu den alten Argumenten hinzugefügt, insbesondere da diese die Herausbildung von immer schlimmeren Krankheitsformen vorhersagt, falls nicht gute Bienenhaltungstechniken eingehalten werden. Die in diesem Beitrag dargelegten Vorhersagen bringen moderne evolutionäre Epidemiologie mit der Honigbienenpathologie auf Verbindung, es steht aber noch an, die praktischen Folgerungen dieser Perspektive in Feldversuchen zu Überprüfen.

Honigbienen / Epidemiologie / Krankheitsübertragung / horizontale Übertragung / vertikale Übertragung

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