

AN ABSTRACT OF THE THESIS OF

Judith Principal de D'Aubeterre for the degree of Doctor of Philosophy in Entomology
presented on December 6, 1996.

Title: Aspects of the Bionomics of the Parasitic Honey Bee Brood Mite, *Varroa jacobsoni*

Oudemans

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Aspects concerning the bionomics of the parasitic honey bee brood mite, *Varroa jacobsoni* Oudemans were investigated. Mite mortality is great during the winter season when the host colony is not rearing brood, appearing to be independent of the mortality of its host. In winter period, no significant association between the number of dead mites and the number of dead adult workers was observed. It appears that the mites are dying by factors other than the host death.

Drifting drones facilitate the horizontal transmission of *Varroa jacobsoni* mites between colonies, especially in modern beekeeping in which managed colonies are kept similarly hived and close together. A great tendency of drones to drift among colonies was observed. A significant correlation was found in the rate of mites per drones and the number of drones in the colonies. It was concluded that the transmission of *Varroa jacobsoni* among colonies *via* drifting drones is a common mechanism for the transmission of mites.

The relationship between mite load and the size of the honey bee brood host was investigated. The data showed significant statistical differences between the infestation rate of the mite that is, number of female mites per infested pupae and the size of the worker brood nest of its host. With a high number of worker cells in the colony, the mite load is lowered.

Feeding activities of *V. jacobsoni* causes a great impact on *A. mellifera* colony survival not only through physical damage caused by this mite but also through transmission of various entomopathogenic agents responsible for the outbreak of secondary diseases in the colony. I concluded that mites fed on adult bees during summer time. It appears that the frequency of mite feeding on adult bees at this time is low, suggesting that probably the mite feeds only for maintenance and survival rather than for reproduction.

**Aspects of the Bionomics of the Parasitic Honey Bee Brood Mite, *Varroa jacobsoni*
Oudemans**

by

Judith Principal de D'Aubeterre

A THESIS

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Judith Principal de D'Aubeterre

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DEDICATION

This dissertation is dedicated to my mother for all her love and guidance which has led me to reach success in my entire life.

ASPECTS OF THE BIONOMICS OF PARASITIC HONEY BEE BROOD MITE, *VARROA JACOBSONI* OUDEMANS

CHAPTER I INTRODUCTION

The parasitic honey bee brood mite *Varroa jacobsoni* Oud. has been known as an ectoparasitic mite infesting *Apis cerana* since 1904 (Oudemans, 1904). *V. jacobsoni* is classified as belonging to the order Parasitiformes, suborder Mesostigmata, family Varroidae (Delfinado and Baker, 1974). The parasite has spread throughout Asia from its native host, *A. cerana*, to the introduced *A. mellifera* due to beekeeping practices and man's intervention. It has been introduced to Europe, Africa, and the Americas, and was first reported in North America from Wisconsin in 1987 (Anonymous, 1987). Only Australia and New Zealand are currently considered to be free of *Varroa*. Considering its cosmopolitan distribution, parasitism by *V. jacobsoni* is now considered the major problem for the beekeeping industry throughout the world.

Mite parasitism of honey bees is a great threat in countries where agriculture is dependent on honey bee pollination activities. In the United States, bee pollination services are required for many crops. These activities add an estimated \$15 billion to the value of United States food crops each year (Adams, 1995). In addition, pollination of hay and seed crops for livestock consumption makes possible the meat and dairy industries which are estimated to be worth another \$35 billion. These figures mean that honey bees contribute to about one-third of the total value of the United States food supply. Consequently, mite parasitism has a great impact on the United States economy.

Varroa jacobsoni and *Acarapis woodi* (Rennie) are considered very harmful to colonies due to the damage that these parasites cause to the adult workers and brood (Akkratanakul and Burgett, 1975; Burgett and Krantz, 1984). *V. jacobsoni* may be found on adult honey bees between the overlapping abdominal sternites. The female mite pierces the intersegmental membranes with its chelicerae to feed on the haemolymph of the adult bee. Mite reproduction occurs only in brood cells.

V. jacobsoni causes severe damage to infested honey bees colonies (Morse et al. 1979 & De Jong et al. 1982). Signs of wing deformation have been observed in lightly infested colonies (Marcangeli et al. 1992) as well as in heavily infested ones (De Jong et al. 1982). Although these wing deformations have been attributed solely to the feeding activities of the mite, the presence of a virus, the deformed wing virus (DWV), has been described on newly emerged infested bees (Ball, 1993). In addition, *V. jacobsoni* has been found to be a vector of acute paralysis virus (APV) in infested honey bee colonies (Ball, 1985, 1988). Similarly, when a young bee emerges from an infested brood cell, a marked reduction in weight compared to their uninfested sisters has been reported (De Jong et al. 1984). Furthermore, these authors stated that this weight reduction seems to be correlated with an increased number of mites. Kovac et al. (1988) measured the life span of infested bees in relation to the season and the extent of mite infestation. They found that, during the summer, newly emerged infested bees always had a shorter mean life span than their uninfested sisters. Similarly, De Jong and De Jong (1983) reported reductions of 34%-68% in the mean adult life span of infested workers. Another negative effect associated with *V. jacobsoni* infestation in honey bee colonies, documented by Weinberg et al. (1985), is the change in haemolymph protein composition of infested pupae. These

authors found that total protein concentration decreased with an increase in the number of mites and that low molecular weight protein fractions were depleted. However, they could not demonstrate whether the depletion of certain constituents was due to the requirement of the mite for specific type of protein in its diet.

The honey bee tracheal mite, *A. woodi* (HBTM) was first detected in the United States in Texas in 1984 (Delfinado-Baker, 1984). This microscopic endoparasite feeds and reproduces inside the tracheae of adult honey bees, shortening the life span of the infested workers (Royce and Rossignol, 1990). Beekeepers have reported high rates of colony losses in many parts of the United States ever since the discovery of *A. woodi*. This increase in colony mortality has been attributed to tracheal mites (Furgala et al. 1989; Burgett, 1993, 1994, 1996). Similar observations were made by Otis et al. (1986) in *A. mellifera* colonies in New York. These authors reported an increase in winter mortality in colonies with over 60% mite infestation. For the Pacific Northwest states of Oregon and Washington, Burgett (1994, 1996) has documented an average Winter mortality of ca. 22% during the period from 1989 to 1996.

Many potential acaricides have been tested to control mite populations in honey bee colonies all over the world. Most of these compounds have the potential to contaminate bee products, and overuse and misuse will likely result eventually in the development of mite resistance to currently registered materials. Presently, the only legal acaricide that may be used in North America to control *V. jacobsoni* is fluvalinate-impregnated plastic strips which kill mites without injuring bee hosts. For HBTM, menthol fumigation has been found to be effective under rather rigid environmental

conditions (Wilson et al. 1990). More recent studies have reported plants extracts to be effective to control these mites (Calderone and Spivak, 1995).

In order to reduce the use of chemicals to control mite populations in honey bee colonies, different management and biotechnical techniques have been developed by beekeepers and researchers. Some of them, such as restricting brood rearing, using drone brood as a trap, and the removal of drone brood are quite effective but time consuming and unsuitable for commercial beekeepers.

Another approach for controlling *V. jacobsoni* populations is utilizing the natural resistance developed by honey bees against it. Peng et al. (1987) reported for the first time the resistance mechanism of the Asian honey bee (*Apis cerana*) to *V. jacobsoni*. The authors stated that, through the mechanisms of auto- and allogrooming, adult workers remove and kill the mites from themselves and from their infested siblings. These findings provide evidence of adaptation between the parasite and its natural host, a concept later supported by other researchers (Rath and Drescher, 1990 ; Boecking and Drescher, 1991; Boecking et al. 1993). However, *A. mellifera* is an alternative nonadapted host, and the host-parasite relationship is not in equilibrium as in *A. cerana*. There are some investigations indicating the occurrence of *V. jacobsoni* tolerance in Africanized and European honey bees from Brazil, Tunisia and Uruguay (De Jong et al. (1984); Camazine, 1986 ; Ruttner et al. (1984) ; Rosenkranz and Engels, 1994). These reports provide evidence of a slight adaptation between the parasite and *A. mellifera* due to reduced fertility of female mite in worker brood compared to the successful reproduction of the parasite in drone brood.

This dissertation evaluates some aspects of the population dynamics of *V. jacobsoni* in an attempt to better understand its relationship with honey bees and to look for biotechnical measures of control to reduce the chemical burden presently found throughout the world in *A. mellifera* colonies. Chapter II examines the feeding behaviour of the parasite by using a stable isotope under laboratory conditions. Chapter III evaluates the overwintering mortality of the mite in comparison to the mortality of the honey bee host. Chapter IV measures the mite infestation rate through the year in relation to size of the brood host under field conditions. Finally, chapter V examines the movement of the parasite by drifting drones under field conditions.

OBJECTIVES

Varroa jacobsoni has become one of the most destructive pests of the western honey bee due to its ability to build up populations to a level which is detrimental to the colonies. Population dynamics and reproduction of this parasite in honey bee colonies depend on several factors which are inherent to host-parasite relationships. Little data are available on feeding behaviour of the mite, overwintering and summer mortality, and how mechanisms such as robbing, swarming, absconding and drifting influence mite dispersal between colonies. It is unclear why some mites do not reproduce even if there is brood available in the colonies, while other female mites reproduce immediately. Likewise, there are no precise data for understanding how many times a mother mite enters the brood cells to reproduce.

The main goal of this work is to clarify the population dynamics of *V. jacobsoni* in order to reduce the need for application of miticides in honey bee colonies, and to find a better way to implement suitable methods of control. Therefore, the specific objectives of this dissertation are:

- A) To evaluate the feeding behaviour of *V. jacobsoni* in broodless colonies.
- B) To examine whether the overwintering mortality of the mite is dependent on the overwintering ability of its host.
- C) To evaluate whether mite load remains constant in relation to brood host size.
- D) To determine whether drifting drones are important as a mechanism of mite dispersal.

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REVIEW OF THE LITERATURE

The mite *Varroa jacobsoni* Oudemans is an external parasite of the eastern honey bee *Apis cerana* F, its original host, and the European honey bee *Apis mellifera* L, a more recent host. *V. jacobsoni* is able to reproduce successfully only in drone brood of *A. cerana*, and although it sometimes enters and feeds on worker brood cells, no offspring are produced (Koeniger et al. 1983). However, recent studies have reported successful reproduction of the mite in worker brood cells of *A. cerana* in South Korea (De Jong, 1988). *V. jacobsoni* parasitizes adults as well as the immature stages of its hosts. It feeds and disperses on adult bees and reproduces on bee pupae. In *A. mellifera*, which serves as an alternative host (Ifantidis and Rosenkranz, 1988), it is able to reproduce in both drone and worker brood. The mite population density in *A. mellifera* may reach such high levels that the colony dies if control measures are not applied by the beekeepers (Delfinado-Baker et al. 1995). The mite was first described by Oudemans (1904) from colonies of *A. cerana* in Java. It is now considered one of the most serious pests of the beekeeping industry worldwide (Akranakul and Burgett, 1975). *Varroa* infestation of honey bee colonies has become a subject of concern to beekeepers throughout the world due to the ability of the mite to build up population levels very rapidly (De Jong et al. 1984), and cause severe losses in colony numbers.

World distribution of *V. jacobsoni*

Varroa jacobsoni is endemic to *A. cerana* in countries of the Far East, but it was not recognized as a parasite of *A. mellifera* until the 1960's. *A. mellifera* originally became

contaminated by close contact with *A. cerana* colonies because beekeepers sought to strengthen their colonies in the Philippines by introducing sealed *A. cerana* brood into their *A. mellifera* colonies. These colonies, which at the very beginning were good producers, later succumbed to *V. jacobsoni* (Morse, 1969).

V. jacobsoni was reported in Europe in the early 1970's. Two invasions of Europe have been reported (Griffiths and Bowman, 1981). The mite was transported directly from Pakistan into Germany, on colonies of *A. cerana* imported for research purposes. There also was a slow invasion from the eastern to the western Europe (Griffiths and Bowman, 1981). Movement of *V. jacobsoni* into Russian bee colonies began when beekeepers from European Russia moved to the Primorski region in far eastern Russia, where *A. cerana* is indigenous. However, it is not clear when the mite was first observed in *A. mellifera* colonies in that region. Apparently, *A. mellifera* queens were exported to western USSR from the Primorski region and they carried the mites. By 1965, *V. jacobsoni* was widespread in *A. mellifera* colonies in western USSR (De Jong et al., 1982). The invasion of the mite into South America was reported in 1971 when Japanese beekeepers shipped *A. mellifera* queens to Paraguay. It is believed that all subsequent mite dispersal in South America was the result of this incipient introduction (De Jong et al. 1982). The parasite was first discovered in the United States in September 1987 (Anonymous, 1987a) and quickly spread throughout all major beekeeping regions to the point where it is now considered nationally cosmopolitan. Only the state of Hawaii is felt to be free of *V. jacobsoni*. Currently, the mite is found throughout Asia, Europe, and the Americas. The only mite-free areas are Australia and New Zealand (Delfinado-Baker & Peng, 1995).

Spread and dispersal

The spread of *V. jacobsoni* throughout the world has been facilitated by beekeepers, beekeeping management, and aspects of the biology of the mite. Activities of the bees such as robbing, drifting and swarming also play an important role in dispersing the mite. These activities may be important in inter-colony transmission, especially in managed colonies where beekeepers locate them too close one to another. Drifting drones for instance, may be very important for the transmission of *V. jacobsoni* from infested colonies to uninfested colonies. Phoretic female mites exhibit a strong preference for drones (Huttinger et al. 1981; Kraus et al. 1986). Similar observations have been made by Ritter and Schneider-Ritter (1988) with *Tropilaelaps clareae* Delfinado and Baker. These authors believe the preference for drones to be an adaptive behaviour for the mites to avoid the grooming activities of worker bees. It has been suggested that mites on adult hosts disperse to new colonies (Rath, et al. 1991). They attach to specific areas of the bee's body; for example, between the lateral intertergites III and IV of *A. cerana* workers and drones and *A. mellifera* workers (Delfinado-Baker et al. 1992). This assists the mites in avoiding grooming activities by the bees and provides a secure site during the phoretic period. The mite's body has well developed structural adaptations for attachment in order to increase efficiency of phoretic dispersal. These include a rounded and well sclerotized body dorsoventral flattening, and powerful legs with large pretarsal ambulacra. (Delfinado-Baker et al. 1992).

Life cycle and reproduction

The life cycle of *V. jacobsoni* includes: larvae, protonymph, deutonymph and adult. Ovoviviparity is a characteristic of *V. jacobsoni* where the eggs are retained in the genital tract (uterus) of the female mite, and embryonic development completed. Following eclosion of the six-legged larval stage, further development proceeds to the protonymph and later to the deutonymph and adult. The duration from egg to adult has been calculated to be 6.0-6.2 days for the female mite and 6.8-6.9 days for the male mite (Ifantidis, 1990 ; Rehm and Ritter, 1989). The female begins her reproductive cycle upon entering a brood cell when the host larva is between 5-5 1/2 days old just prior to the time when the cell is sealed by the worker bees. Once inside the cell, the mite burrows into the larval food mass at the base of the cell. When the bee larva eats the food, the mite is liberated and starts feeding on the larva of the bee, and later on the prepupa (Fries, 1993). Mite oviposition begins 60 hours after the cell is sealed. Eggs are laid at a rate of one each 30 hours (Ifantidis, 1983, 1984). The first egg develops into a male and the rest of the eggs normally into females. On average the female mites deposit three to four eggs in the cells (Ifantidis, 1984). Transfer of semen from males to females takes place only in the sealed brood cells, and when the bee emerges the male and the immature females are lost. Apparently, the male does not feed and dies after the adult bee emerges from the cell (Ifantidis, 1990 ; Rehm and Ritter, 1989). When the bee emerges, the adult mite F_1 and the foundress female transfer to adult bees and are considered at that time to be phoretic (Rath et al. 1991).

Factors influencing reproductive success of the mite

Mite reproduction inside the brood cells is a complex process that is influenced by factors inherent to the parasite including age, physiological conditions and fertility (Ifantidis, 1988), as well as by host factors including host biotype (Camazine, 1988), postcapping period (Moritz and Hanel, 1984), and environmental conditions including climate and season of the year (Marcangeli et al. 1992). The reproductive success of *V. jacobsoni* depends on many factors. Mite reproduction occurs only when there is brood available in the colony. Brood cells are invaded by the mites during a period of 15-20 hours and 40-50 hours in worker and drone brood respectively, preceding cell capping by worker bees (Boot et al. 1992). There is strong preference for the mites to invade drone brood cells (Koeniger et al. 1983; Issa et al. 1984; Issa et al. 1985 ; Le Conte et al. 1989; Fuchs, 1990). Studies done by many researchers both under field and laboratory conditions have demonstrated this preference for drone brood (De Jong, 1984; Rosenkranz et al. 1984; Otten and Fuchs, 1989; Schulz et al. 1983; Tewarson, 1983). Fuchs (1990) found a preference factor of 12.1 for drone brood when a specific amount of drone brood was available. Moreover, the author suggests that this preference factor is equivalent to 92% of the mites entering the drone brood. Many explanations have been proposed to explain this phenomenon. Aliphatic esters may be involved in mite recognition of drone brood cells (Le Conte et al. 1989; Trouiller et al. 1992). These authors isolated and identified ten straight-chain fatty acid esters from bee larvae extract, some of which attracted *V. jacobsoni* females to the brood cells. More recent studies

(Trouiller et al. 1994) reported that these substances are secreted by worker and drone brood a few hours before the cell is capped.

Another factor influencing reproductive success of the mite inside the brood cells is the diminished ability of some female mites to reproduce in worker cells. That is, there is a proportion of female mites that are unable to reproduce (infertility). This percentage is relatively high in tropical and subtropical Latin American countries (De Jong, 1984; Camazine, 1986, 1988). Lower infestation rates due to mite infertility also was reported in colonies in Uruguay, (Ruttner et al. 1984), who found that 60% to 90% of the female mites in worker cells did not produce offspring. In Brazil, where *V. jacobsoni* has been present since 1972, low stable infestation levels have been reported (De Jong et al. 1982; Goncalves, 1987; Moretto et al. 1995). On the other hand, lethal infestations have been reported in Argentina where the genetic composition of *V. jacobsoni* is the same as in Brazil (Moretto et al. 1991). This suggests that factors other than the genetic composition of the mite, climate, and/or bee race might be involved in this phenomenon.

The influence of parasitic intensity on mite reproduction has also been mentioned as a factor that may regulate mite population size in *A. mellifera* colonies. Studies have demonstrated that the reproductive rate of the mite decreases when the number of mite per cells increases (Fuchs and Langenbach, 1989a). This suggests that density dependent factors may act as regulatory mechanisms on mite population in the colony. The phenomenon of parasitic intensity was also reported by Marcangeli et al. (1992) in temperate Argentina. These authors found that the number of reproducing mites decreased while the density of the mite increased during autumn. However, during the spring season, the number of reproductive female mites was not significantly different in

relation to mite parasitic intensity. Further studies done by Eguaras et al. (1994) on the influence of the parasitic intensity on mite reproduction in worker brood cells of honey bees *A. mellifera* in Argentina have demonstrated a decrease in the mite reproductive rate from about three offspring per mite at 1 mite/cell to one offspring per mite at 6 mites/cell. In addition, the number of females which reached maturity also decreased.

Honey bee hormones, especially juvenile hormones, have been proposed as a regulatory mechanism of reproduction for *V. jacobsoni*. Studies done by Hanel and Koeniger (1986) have shown that drone larvae of both *A. cerana* and *A. mellifera* contain more than 5 ng/ml juvenile hormone in the haemolymph during the first 60 h after brood cells are sealed. Worker brood of *A. mellifera* contains between 3-7 ng/ml whereas *A. cerana* worker brood does not reach 1 ng/ml during the first day after the cell is sealed. Moreover, the authors found that concentrations lower than 4 ng/ml seem to be one factor that prevents reproduction of the parasite. Rosenkranz et al. (1990) and Rosenkranz et al. (1993) refuted the idea that juvenile hormone is involved in regulation of mite reproduction. These authors found no differences in titer of juvenile hormone III in the haemolymph of L5 instars in *A. cerana* and *A. mellifera*, suggesting that juvenile hormone does not regulate mite reproduction.

Resistant mechanisms of *A. mellifera* toward *V. jacobsoni*

Resistant mechanisms of honey bees toward *V. jacobsoni* have been a major area of interest among many researchers. Observations on bee behaviour, specifically grooming, have contributed some understanding to resistance. Grooming behaviour

performed by the bees includes the following activities: antenna and head cleaning, grooming of the mouthparts, legs, wings bases, thorax and abdomen. These activities are carried out by the bees to remove foreign matter from the body, clean and straighten wings, manipulate pollen, remove ectoparasites, and to spread pheromones about the body (Naumann, 1991). In addition to self-cleaning, and nestmate, and group cleaning, a grooming dance is performed by the bees. This behaviour was found to contribute to the efficient removal of mites from the body of the adult host (Peng et al. 1987). Comparisons of grooming behaviour between *A. cerana*, *A. mellifera* and *A. dorsata* workers also have been reported (Buchler et al. 1992). The authors used different sources of *V. jacobsoni* to infest workers of these three bee species in Thailand. They found that workers of *A. cerana* respond more vigorously to the presence of *V. jacobsoni* than does *A. mellifera* when mites are placed on their thoraces. According to the authors, *A. cerana* workers caught mites with their mandibles, and killed them while in *A. mellifera* this behaviour was never observed. This suggests that *A. cerana* workers are adapted to removing the mites from their bodies. Similarly, *A. dorsata* exhibited an intensive and long lasting auto-grooming almost immediately after a mite was placed on the bee's thorax, whereas with *Tropilaelaps* mites this response was less frequent (Buchler et al. 1992).

Removal by *A. mellifera* of diseased larvae from colonies infected with American foulbrood has been known (Woodrow, 1941). Similar behaviour has been reported by bees in the removal of mite-infested brood in *A. cerana* and *A. mellifera* colonies (Rath and Drescher, 1990; Boecking et al. 1993; Boecking and Drescher, 1990, 1991). Apparently, the removal behaviour in *A. cerana* is highly effective in reducing the overall

mite load of colonies (Rath and Drescher, 1990). These authors have shown that 98% of artificially infested worker brood were removed within five days of infestation. In contrast to *A. cerana*, *A. mellifera* workers were not able to identify and remove brood cells infested with *V. jacobsoni* as frequently as described for *A. cerana*. Further studies have shown that *A. mellifera* workers removed more drone brood cells artificially infested with the parasite compared to infested worker brood (Boecking et al. 1993). A model of parasite removal from the brood of *A. dorsata* workers was postulated by Burgett et al. (1990). These authors suggested that *A. dorsata* workers could detect *T. clareae* and remove infested brood together with the mites. Rath (1992) showed that *A. cerana* workers detect the mite-infested sealed worker cells and remove infested larvae, forcing the mites to reproduce in drone brood cells. This behaviour has been observed in *A. mellifera* as well, where the bees are capable of removing mite-infested drone brood as well as worker brood (Boecking and Drescher, 1989, 1990). The latter authors hypothesized that a pheromone emitted from the brood might be responsible for the behaviour of the bees toward dead, diseased, and mite-infested sealed brood. Consequently, the removal behaviour would interrupt mite reproduction by decreasing the number of female mites that can survive inside the cells, and by killing the immature mites that are developing at the moment of removal of the larvae.

A shorter postcapping period in worker brood is reported to influence the reproductive rate of *V. jacobsoni* inside the brood cells. In *A. mellifera* the duration of the postcapping period in worker brood is ca. 12 days, while in drone brood the postcapping period is ca. 14 days (Jay, 1963). The longer period of postcapping for drones allows for additional F₁ mites to reach sexual maturity inside the brood cells. This

aspect of mite biology is very important in the sense that a shorter postcapping period for the host would provide less time for *V. jacobsoni* to reproduce and consequently, it would lead to a honey bee colony with a reduced mite population. The resistant to *V. jacobsoni* by honey bee colonies of different races has been mentioned by many authors. In Africanized bees a shorter development time compared to European bees has been attributed to be one of the factors that influences a differential reproduction rate. This is due to the fact that many immature deutonymphs fail to reach sexual maturity within the capped brood cells before the adult bees emerge (Camazine, 1986). Studies done by Moritz and Hanel (1984) and Moritz (1985) have shown that the mean duration of the capped period of *A. mellifera capensis* lasts on average 9.6 ± 0.07 days, whereas worker bee cells of *A. mellifera carnica* are sealed at about 12.04 ± 0.03 days. Moreover the authors found that less than 50 % of all reproductive female mites were able to produce only one infective offspring mite at maximum in *A. mellifera capensis* colonies in contrast to 100 percent in *A. mellifera carnica*. They attributed the duration of the postcapping period as the main factor limiting the reproductive success of the mite.

Population dynamics

The population dynamics of *V. jacobsoni* in honey bee colonies involves three primary processes: the entry of the female mite into the worker or drone brood cells; its reproductive success inside these cells and; the mortality of the parasite. It has been documented that female mites enter worker or drone brood cells ca. 20 h and 40 hours respectively before the cells are capped by the worker bees (Boot et al. 1992). There are

several factors that affect the entry of a female mite into the brood cells. These include: the phoretic period, the availability of brood in the colony, the removal of infested brood and the mite's preference for drones. Other studies have shown differences in the length of the phoretic period of the mite while on the adult bees (Schulz, 1984). This author reported a phoretic period of 4.5 days for old mites, 10.7 days for young mites and, 7.4 days for a mixed population of mites respectively. However, data presented by Woyke (1987) have shown an average phoretic period of 5.9 days and 4.7 days for young mites and mixed mite population respectively. Brood available in the colony would influence the entry of female mites into the brood cells as well (Fuchs, 1990). Apparently, mites require a phoretic period on the adult bees for a certain period of time before reproduction can occur (Schulz, 1984; Fuchs, 1985). It has been observed that some mites remain on adult bees for a few days before invasion of the brood, others prefer to reproduce immediately after being released with the emerging bee (Schulz, 1984). This suggests that other factors may be involved in mite reproduction.

Mite mortality has been mentioned as another factor that would influence the mite population size in a colony. Peng et al. (1987) have reported that *A. cerana* workers kill the mites by grabbing them with their mandibles, suggesting that the grooming behaviour performed by the bees limits the mite population size. Avitabile (1978) reported that 50% of the bees die during winter, suggesting that the mortality of the mite in the winter cluster might be about 50%. Other studies done by Fries et al. 1991 indicated that the number of mites found on live bees, was similar to the number of mites found on dead bees that fall from the winter cluster, which suggests that the mites do not migrate from dying hosts. Similar observations were made by Ritter et al. (1989) in *A. mellifera carnica*, which

indicated that *V. jacobsoni* remains on their host even when the bees move to different temperature zone within the winter cluster.

Up to the present time, the data available on the mortality of the mites living on the adult bees during summer and winter as well as, the intrinsic mortality of the parasite are limited. Further studies in the biology of the mite need to be done in order to fully understand the population dynamics of this parasite, which endangers honey bees throughout the world.

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CHAPTER II
**EVIDENCE OF FEEDING BY *VARROA JACOBSONI* OUDEMANS ON ADULT
WORKER HONEY BEE, *APIS MELLIFERA*, DURING THE SUMMER**

ABSTRACT

Feeding behaviour of *Varroa jacobsoni* Oudemans was measured in order to determine whether mites fed on honey bee adults during the summer period when active brood rearing is taking place. Worker bees were maintained in cages provided with a screened lid to allow the bees to be fed. After 6 hours of food and water deprivation for both host bees and mites, the mites were placed inside the cages together with the worker bees. Honey bees were allowed to feed on 20 ml of sugar solution labeled with D-Glucose-1-¹³C and then placed in an incubator at 20°C for 24 hours. Samples of workers and mites were taken every six hours, and the amount of ¹³C in mite biomass and bee haemolymph was determined by mass spectrometry. After 24 hours, a quarter of cages containing mites were tested positive for ¹³C uptake, suggesting that mites had fed on adult honey bees hosts. In addition, the novel technique of ¹³C-labeling can be successfully used as a marker for both bees and mites with no apparent detrimental effects on their biology.

INTRODUCTION

Varroa jacobsoni Oudemans, a native parasite of *Apis cerana* F. in southeast Asia is not destructive to *A. cerana* due to the ability of the bee workers to recognize and remove the mites from their bodies and from the infested brood (Peng et al. 1987). As a rule, *V. jacobsoni* reproduces only in drone brood of its native host, but in worker brood

the reproducing female lacks the ability to produce offspring (Ritter, 1981). In contrast, the mite reproduces in drone brood as well as in worker brood of the non-adapted host *A. mellifera*, thus potentially causing lethal damage to the infested colonies if they are not treated.

The mite feeds on haemolymph of adult bees and developing pupae, causing loss of weight in worker bees (De Jong et al. 1982a), shortening the life span of forager bees (De Jong and De Jong, 1983), and reducing blood protein levels (Weinberg and Madel, 1985). It is generally acknowledged that the mite has a great impact on the bee mortality in an infested colony. Feeding activities of the mites during the brood stages also produces detectable losses (15-50%) in haemolymph protein levels and total haemolymph volume of the newborn bees (Smirnov, 1978). In addition, morphological changes such as wing and abdomen deformations have been reported (Akratanakul and Burgett, 1975; De Jong et al. 1982; Marcangeli et al. 1992). These changes may be associated with secondary pathogens such as viruses, fungi and bacteria that may be vectored by *V. jacobsoni* feeding activities (Ball, 1983, 1985 ; Smirnov, 1978).

Various techniques for rearing mites *in vitro* on artificial diets have been developed (Bruce et al. 1991; Bruce et al. 1988; Rath, 1991). However, no precise data concerning seasonal feeding habits of the mite on adult bees are available. Because *V. jacobsoni* does not exhibit physogastry after feeding, it is difficult to assess feeding frequency. The goal of the present study was to evaluate whether *V. jacobsoni* feeds on adult bees in broodless colonies of *A. mellifera* during summer.

MATERIALS AND METHODS

A total of 450 honey bee workers were removed from colonies maintained at the Honey Bee Laboratory at Oregon State University. Approximately 112 workers were kept in each of four small cages without food for a period of six hours. The cages had screened lids to allow the bees to feed. Female mites, removed from drone brood combs from infested colonies, were inoculated at a rate of one mite/adult worker bee. Bees in three of the four cages were then allowed to feed on 20 ml of a glucose solution labeled with the stable isotope (D-Glucose-1-¹³C, 99 atom-% enrichment) for a period of approximately 24 hours. A control cage was similarly manipulated but not labeled.

Every six hours, samples of bee haemolymph of ca. 10 µl were collected in micropipettes, emptied into 6x4 mm tin capsules coated with filter paper, placed into a microtitration plate and assayed at the Stable Isotope Research Unit in the Department of Soil Science at Oregon State University to determine the amount of ¹³C present. Samples of 6-8 adult female mites taken from these bees were also checked for the label using mass spectrometry analysis. The instrument used to analyze the samples in this experiment was the Europa Scientific ANCA-MS automated mass spectrometer which is capable of analyzing with a precision of +/- 1‰ δ (0.0003 atom % ¹⁵N) , and 0.2‰ δ ¹³C (0.0002 atom % ¹³C), at natural abundance levels.

RESULTS

The amount of ¹³C (δ values) in the haemolymph of the bees as well as in mites was measured using mass spectrometry analysis in order to evaluate the proportion of

mites feeding on haemolymph of worker bees. Stable carbon isotope ratios are usually expressed in delta notation as the following formula: $\delta^{13}\text{C} (\text{‰}) = 1000(\text{R sample} - \text{R standard}) / \text{R standard}$, where R sample is the ratio of the heavy to the light isotope measured for the sample and R standard is the equivalent ratio for the standard.

Table II. 1. shows that the bee haemolymph of worker bee samples had greater part per thousands of ^{13}C than the control relative to the standard PDB at natural abundance levels, which means the haemolymph was highly labeled. The standard PDB is the cretaceous carbonate fossil, *Bellemnitela americana*, from the Peedee Formation in South Carolina, USA (abbreviated to PDB). It has a $(\delta = 0\text{‰})^{13}\text{C}/^{12}\text{C}$ ratio = 0.0112372.

Table II. 2. shows the amount of ^{13}C expressed in (‰) detected in *V. jacobsoni* biomass, the δ values obtained here were negative because control bees and mites are slightly depleted in ^{13}C relative to the PDB. In the case of Table II. 2., if mites had fed on adult workers, any significant increase in ^{13}C values compared to control would suggest that mite feeding had taken place. I therefore calculated the confidence intervals of ^{13}C natural abundance in non-labeled treatments and compared it to the groups. Mites from labeled samples that were greater than the upper 95% confidence intervals were considered positive; that is, mites fed on bees (Table II. 2).

Table II. 1. $\delta^{13}\text{C}$ + (‰) detected in the haemolymph of worker bees.

Time	Cage 1	Cage 2	Cage 3	Control
6 h	10.86	5.31	12.15	-21.50 <i>a</i>
12 h	2.98	29.30	27.61	-21.00 <i>a</i>
18 h	25.21	20.21	44.32	-17.48 <i>a</i>
24 h	6.98	5.39	11.77	-20.88 <i>a</i>

a Negative delta values are obtained because control bees are slightly depleted in ^{13}C relative to the PDB.

$\delta^{13}\text{C}$ values relative to standard (0+ = 1.108 atom % ^{13}C).

1+ difference = 0.001108 atom % ^{13}C at natural abundance.

Table II. 2. $\delta^{13}\text{C}$ (‰) detected in *V. jacobsoni*.

Time	Cage 1	Cage 2	Cage 3	Control
6 h	-17.77 <i>ab</i>	-27.71 ^b	-30.92 ^b	-31.38 ^b
12 h	-28.05 ^b	-32.79 ^b	-29.14 ^b	-31.32 ^b
18 h	-26.89 ^b	-26.94 ^b	-27.88 ^b	-37.58 ^b
24 h	24.59 <i>a</i>	-24.18 <i>ab</i>	-35.93 ^b	-29.35 ^b

^a Samples that fell outside 95% confidence intervals (-26.72, -38.09).

^b Negative delta values are obtained because control mites are slightly depleted in ^{13}C relative to the PDB.

PDB $^{13}\text{C}/^{12}\text{C}$ ratio = 0.0112372 ($\delta = 0\text{‰}$)

DISCUSSION

Given that a quarter of the mite samples were positive, I conclude that *V. jacobsoni* fed on adult worker honey bees during the trial period of 24 hours. However,

although mites did feed on bees, feeding frequency appeared to be low. Since only three of 12 samples were positive over the 24 hour feeding period, and each sample had 6-8 mites, the actual frequency/mite was small. Normally, the inverse of the incidence of feeding for a mite (here an apparent 25%/day) would be the frequency of feeding, or once every 4 days for a single mite. This estimate is, however, a conservative one because there were 6-8 mites in each sample. Given that one mite may make the sample positive, frequency is undoubtedly much less than estimated here. Therefore, although mites feed on honey bee workers, the parasitological impact may be negligible and feeding may be related mostly to daily survival rather than to reproduction.

My conclusions support the assumption made by Smirnov (1978) who stated that *V. jacobsoni* mites feed little on workers bees in summer. This study is therefore the first documentation of summer feeding frequency. It should be noted, however, that this is not a true longitudinal study, and that feeding incidence or even prevalence cannot yet be estimated accurately. However, it is apparent that mites do feed, albeit infrequently.

SUMMARY

Based on these results I conclude that *V. jacobsoni* fed on adult worker bees, albeit at low frequency. In addition to my biological conclusions, this study is the first to introduce and demonstrate the power of ^{13}C -labeling in insects. The technique may be of great value as a supplement or complement to other labeling techniques, such as ^{14}C radio-labeling, fluorescent dyes, rubidium-labeling etc. Most notably, ^{13}C -labeling is non-toxic, quantitative and extremely sensitive. It is very important to emphasize that we now have

the tool to look at feeding behaviour at different times of the year when mites are on adult hosts and this may have control implications because the mites are more vulnerable on adult hosts than on brood host.

The next step in this investigation would be to repeat the study longitudinally, assess rates of feeding of individual mites, and then document actual rate of transfer of material from host to parasite, thus obtaining parasitological load. The same methodology could be used for comparative feeding assessments on the brood host. The correct and quantitative measurement of parasite load would be a major contribution to our understanding of honey bee parasitism in general. Our current knowledge is based primarily on damage documented at the colony level, and is therefore indirect.

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CHAPTER III
OVERWINTERING MORTALITY OF *VARROA JACOBSONI*
OUDEMANS IN COLONIES OF THE HONEY BEE, *APIS MELLIFERA* L.

ABSTRACT

The mortality of *Varroa jacobsoni* Oudemans and adult workers of *Apis mellifera* L. were studied during the winter months in broodless colonies of *A. mellifera*. All observed dead mites and dead bees that fell from winter clusters were examined on a daily basis. Dead mites on dead bees, as well as mites found dead on a plastic sheet directly below the clusters also were recorded. The data showed no evidence of a significant association between the dead mites and the dead bees (P-value = 0.08 ; $\chi^2 = 3.0632$). It was concluded that mite mortality is not linked to adult bee mortality.

INTRODUCTION

The population dynamics of *Varroa jacobsoni* Oud. is influenced by several factors that contribute to mite population growth throughout the year, especially when there is brood available in the colony. Mortality of mites on adult bees seems to have little effect on mite population growth during a period when brood rearing is taking place. However, during the winter period when brood is not present, and the mite population is maintained on adult bees only, the impact of adult female mite mortality on its population dynamics would be high during these broodless periods. It has been reported that in temperate climates during winter periods, the mites are distributed randomly on adult bees within the winter cluster (Ritter et al. 1989) and they prefer to stay on the ventral left side of the

abdomen of adult bees (Fernandez et al. 1993). At this time there is a period in which the host colony remains broodless. Consequently, neither the parasite nor host experience population growth. In regions with cold winters, more than 50% of the bee population is estimated to be lost before the number of bees increases again in the spring (Avitabile, 1978). One would therefore conclude a concurrent decline in mite population.

Studies done by Muller (1987) indicated that mite mortality during the winter occurs when host bees fall from the winter cluster, suggesting that the mites are unable to switch to a new host. Korpela et al. (1992) have demonstrated an average loss of mites during winter of over 40% in *A. mellifera* colonies kept in southeast Finland under conditions of no infestation pressure from outlying mite-infested apiaries. Calatayud et al. (1994) measured the survival rate of phoretic *V. jacobsoni* in broodless *A. mellifera* colonies. Their results showed maximum life span of *V. jacobsoni* ranging from 80 to 100 days and a mean life expectancy of 31 days under broodless colony conditions.

Accordingly, I measured the mite and bee mortality in broodless colonies of *A. mellifera* during winter with the purpose of determining whether or not mite mortality is associated to host mortality.

MATERIALS AND METHODS

Three colonies were maintained in movable deep frame hive bodies. Each colony was composed of four frames covered by adult workers. The bottom board in each colony was removed and replaced with a white plastic sheet coated with an oil to prevent removal of the mites by the bees. These colonies were fed with three frames containing

pollen and nectar and placed in a dark cold room to avoid infestation variation caused by robbing or drifting bees from external infested colonies. The temperature inside the room was monitored daily and averaged 5.1 °C.

At the beginning of the experimental period the total population of adult bees in each colony was estimated as described by Burgett and Burikam (1985). The total number of mites in each colony was estimated by multiplying the mite load in adult bees by the total number of adult bees estimated in the colonies. All dead bees and dead mites falling from the clusters were collected daily during 44 day period from November 8 to December 21, 1994. The dead bees were placed in small plastic jars and transported to the laboratory for later examination. The bees were washed in the laboratory with hot water and agitated vigorously for approximately four minutes to facilitate dislodgment of the mites from the abdominal tergites of the bees. All mites found dead on bee bodies, as well as dead mites found on the bottom board plastic sheet, were counted. The data were analyzed using the Mantel-Haenszel chi-square test (Ramsey and Schafer, 1995).

RESULTS

A Mantel-Haenszel chi-square test analysis was done to assess whether mite mortality is associated to bee mortality. No significant association between mite and bee mortality was shown (P-value = 0.08 ; $\chi^2 = 3.0632$) (Table III. 1). Data describing the populations of mites and bees estimated in the colonies, as well as the number of dead mites and dead bees collected from the bottom board of the colonies from Nov. 8 to December 21, 1994 are summarized in tables III. 2 and III. 3.

Table III. 1. Mantel-Haenszel chi-square test results for dead bees and dead mites collected during 44 day period (Nov. 8 to Dec. 21, 1994).

a. Colony 1, b. Colony 2, c. Colony 3.

a.

	< 50 dead bees	≥ 50 dead bees
< 5 dead mites	16	18
≥ 5 dead mites	6	4

b.

	< 50 dead bees	≥ 50 dead bees
< 5 dead mites	11	10
≥ 5 dead mites	4	19

c.

	< 50 dead bees	≥ 50 dead bees
< 5 dead mites	8	18
≥ 5 dead mites	2	16

Chi-square = 3.0632, df = 1 , P-value = 0.0801

The number in each cell represents the number of days (out of 44) when both intersecting conditions were met. For example in Table III 1a, for colony 1, there were 16 days when less than 50 dead bees and less than 5 dead mites were found.

Table III. 2. Mite and bee population estimates in the colonies at beginning the experiment (Nov. 8, 1994).

Population	Colony 1	Colony 2	Colony 3	Total
Workers	7,170	7,776	8,502	23,448
Mites	287	389	340	1,016

Table III. 3. Mite and bee mortality during 44 days (Nov. 8 - Dec. 21, 1994).

Population	Colony 1	Colony 2	Colony 3	Total	% dead
Workers	2,407	4,314	3,575	10,296	44%
Mites	197	285	210	692	68%

DISCUSSION

The data presented here support the hypothesis that overwintering mite mortality is not linked to honey bee mortality in colonies of *A. mellifera* during the winter period. This suggests that, in overwintering colonies when brood are not being produced and mite population growth is zero, the cause of mite death may be related to factors other than bee death. Given that mites are dying at a higher rate than bee hosts, factors such as mite behaviour on adult bee hosts within the winter cluster needs to be studied more closely. If mites start moving around on worker bees, when bees change position from the inner shell to the outer shell within the winter cluster, it may be possible for the mites to be knocked off by a passing bee. In addition to this factor, the intrinsic mortality of mites while on the

adult bees within the winter cluster, due to physiological causes such as age and undernourishment, may influence mite mortality.

Previous reports indicate that mites are distributed randomly within the winter cluster (Ritter et al. 1989) and apparently do not leave a dying host (Fries et al. 1991a ; Muller, 1987) when brood are not available in the colonies. Taking into account that *V. jacobsoni* is an alternative, non-adapted parasite for *A. mellifera*, it is possible that the mites may be able to distinguish a dying host when its temperature drops.

Studies done by Omholt et al. (1991) on predicting the degree of infestation of honey bee colonies by *V. jacobsoni* suggested that the size of the winter mite population may be an important factor in whether there will be a rapid increase in mite population growth in honey bee colonies in the following spring. For example, in cases of heavily infested colonies, the parasites which remain alive on adult bees during the winter period, along with the re-infestation caused by drifting and robbing, may cause a great surge in mite population growth and the development of significant infestations early in the spring when the colonies start rearing brood and the mites begin to reproduce.

SUMMARY

Based on the results in this study, I conclude that mite mortality is not strongly linked to bee mortality during the winter period. Apparently, there are other factors that influence mite death during the winter period.

The present study provides further information regarding one of the factors that influences population dynamics of *V. jacobsoni* and may be useful in better understanding

the host-parasite relationship. This knowledge should be taken into account for mite control based on biotechnical methods. However, further studies will be needed to identify some of the other factors that may be involved in the mortality of *V. jacobsoni* during the winter season.

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CHAPTER IV
CHANGES IN INFESTATION RATES OF *VARROA JACOBSONI* OUDEMANS
IN RELATION TO THE BROOD HOST SIZE (*APIS MELLIFERA* L.)

ABSTRACT

The study was conducted at the Oregon State University Honey Bee Laboratory during the period March to October, 1995. Four honey bee colonies were maintained in two deep frame hive bodies and treated with fluvalinate strips for three weeks to reduce mite infestation to an equivalent low level. One week after miticide treatment, sealed brood from a highly infested colony was inoculated into each of the four test colonies. Samples of drone brood and worker brood were taken from each colony monthly. Mite infestation levels (number of invasive female mites/infested pupae) and host brood size were determined on a monthly basis. The data show that, in worker brood, the mite infestation decreased as the number of brood cells increased while in drone brood, the infestation level remained constant (P- value = 0.0125 and 0.3749 respectively).

INTRODUCTION

The parasitic mite, *Varroa jacobsoni* Oudemans, endangers the honey bee *Apis mellifera* L., wherever the bees have been transported by man, with the current exceptions of New Zealand and Australia. This mite lives on adult *A. mellifera* as an ectoparasite but only reproduces inside the capped brood cells of its host, having a strong preference for drone brood (Otten and Fuchs, 1988 ; Fuchs, 1990). The invasion of honey bee brood cells by *V. jacobsoni* takes place from 15-20 h and from 40-50 h before capping in worker

and drone cells respectively (Fuchs and Muller, 1988 ; Boot et al. 1992), and it is considered an important process for determining the time for mite reproduction and mite population growth inside the honey bee colony (Boot et al. 1994).

Studies done by Fuchs and Langenbach (1989) on *Apis mellifera carnica* demonstrated that as the number of foundress mites/cell increases, the number of female offspring /mite decreases within both drone and worker cell types, suggesting the presence of a density-dependent reproduction factor which may limit parasite population growth in the colony. In this study, I measured mite population in brood cells of its host to determine whether mite infestation (*Varroa/pupae*) remained constant as the brood size of the colony increases.

MATERIALS AND METHODS

Research was carried out at the Oregon State University Honey Bee Laboratory from March to October, 1995. Four colonies were used in this study, each consisting of two deep frame hive bodies. Just prior to beginning the study, the test colonies were treated for three weeks with fluvalinate strips to reduce mite infestation to an equivalent low level. During the following week, one frame containing sealed brood from a highly infested colony was inoculated into each treatment colony. All colonies were equalized as much as possible regarding the number of adult bees, brood and food and were managed to prevent swarming. Samples of 50 drone brood cells and 100 worker brood cells on average were taken from each colony each month during the period from March - October, 1995. The brood cells were unsealed and inspected individually under a

dissecting microscope and the number of invasive adult female mites per brood cell were recorded. Concurrent with the sampling of mite infestation, the brood size of the colony was estimated (Burgett and Burikam, 1985; Jeffree, 1958) and the total population of adult female mites in the brood cells was estimated. The data for infested pupae in worker brood, as well as in drone brood, were analyzed using a multiple linear regression model. Before data analyses were performed, infestation rates on drones and worker brood were transformed using log transformation to adjust the error structure of the infested pupae in the cells.

RESULTS

I measured the mite load of *V. jacobsoni* (V/pupae) on the brood of its host to determine whether mite infestation remains constant as the number of brood cells of the host increases. I found significant statistical differences between the infestation of the invasive female mites and the amount of worker brood (P-value = 0.0125), whereas for drone brood no significant differences were found between the infestation of invasive female mites and the size of the drone brood host (P-value = 0.3749). The number of female mites/pupae in drone brood tends to be constant as the host brood size increases. Data concerning the brood size of the honey bee colonies and mite load in worker and drone brood are summarized in tables (IV. 1 - IV. 4).

Table IV. 1. Mite load present in brood cells by colony.

Months	Colony 1		Colony 2		Colony 3		Colony 4	
	IRW ^a	IRD ^b	IRW	IRD	IRW	IRD	IRW	IRD
March	1	1	1.14	3.82	1.71	2.98	1	1.33
April	1	1	1	1	1	2.17	1	1
May	1	1.96	1	2	1	2.04	1	1
June	1.36	3.07	1	2.36	1.17	3.04	1	2
July	1.5	2.5	1	1.6	1	1.89	1	2.28
August	1	0	1.5	0	2.26	0	1.25	0
September	1.47	0	1.2	0	1.47	0	1.25	0
October	1.45	0	1	0	1.76	0	1.33	0
Mean IRWD ^c	1.22	1.91	1.11	2.16	1.42	2.42	1.10	1.52
SD IRWD	0.24	0.91	0.18	1.06	0.46	0.55	0.14	0.59
Mean Log IRWD	0.18	0.54	0.09	0.67	0.31	0.86	0.09	0.36
SD Log IRWD	0.20	0.52	0.15	0.49	0.31	0.22	0.13	0.38

^{a, b} Infestation in worker and drone brood cells respectively (female mites/infest. pupae).

^c Mean number female mites/infested pupae in worker and drone brood cells.

Table IV. 2. Average invasive female mite load by brood type - all colonies.

Months	mites/infest. worker pupae	mites/infest. drone pupae
	AVG	AVG
March	1.21	2.28
April	1	1.29
May	1	2.00
June	1.13	2.62
July	1.13	2.07
August	1.50	^a
September	1.35	^a
October	1.39	^a

^a Drone brood not present in the test colonies.

Tables IV. 1 and IV. 2 show that the mite load was relatively low in worker brood compared to drone brood from March to July. However, a slightly increase in mite infestation in worker brood was observed from August to October and this may be because female mites had only worker brood available for reproducing during this period, a time when drone brood is on a steep decline. The mean and standard deviation of the mite infestation for worker brood was estimated for eight months while for drones the

mean was calculated for only five months because the colonies stopped producing drone brood in July, which is a normal pattern for drone production in temperate regions.

Table IV. 3. Mite population and brood size by type - combined for all colonies.

Months	Worker size AVG ¹	Adult Mites AVG ²	Drone size AVG ³	Adult Mites AVG ⁴
March	9664	1055	2173	725
April	12599	438	2514	189
May	17444	324	2184	1018
June	17589	958	2002	1501
July	13482	965	529	380
August	6767	1546	-	-
Sept.	6219	1924	-	-
October	1603	787	-	-

^{1, 3} Average number of worker and drone cells estimated in the colonies (size).

^{2, 4} Average number of adult females mites estimated in the brood size.

Table IV. 4. Average number of mites per cell type- all colonies combined.

Months	#mites/ worker cell AVG	#mites/drone cell AVG
March	0.11	0.32
April	0.03	0.19
May	0.02	0.29
June	0.07	0.26
July	0.08	0.36
August	0.17	^a
September	0.25	^a
October	0.33	^a

^a Drone brood not present in the test colonies

DISCUSSION

The data analyses presented in this study reveal an inverse relationship between the number of foundress female mites per pupae and the total worker brood population of the host. These results indicate that the higher the number of worker brood cells in the

colony, the lower the mite load per brood cell. This suggests that in cases of severe infestations, mites will disperse among the available cells and maintain an infestation rate at a threshold that may extend the host colony's survival for a longer period. In addition, it is advantageous to mite reproduction because if honey bee brood cells are infested by a large number of mites, brood rearing in the colonies may be interrupted to the point that mite and bee populations will decline rapidly, leading to the death of the system. A higher mite load per brood cell will result in fewer offspring per female mite (Fuchs & Langenbach, 1989 ; Donze et al. (1996).

However, in drone cells the number of adult female mites per infested pupae appears to be relatively constant as the number of brood cells in the colonies increases. This phenomenon may be related to the small size and seasonal production of drone brood in honey bee colony compared to worker brood. Additionally, mites prefer drone brood as a reproductive host, thus ensuring a high rate of female mite reproduction and perpetuation of the mite population and parasitism of drone brood does not directly interfere with the honey bee colony survival.

Many host-parasite relationships may be described by a negative binomial distribution (Crofton, 1971). *V. jacobsoni* displays this distribution in drone cells at low mean infestation rates (Donze et al. 1996), this parasitic relationship would allow some host bee larvae to survive (Begon & Mortimer, 1985).

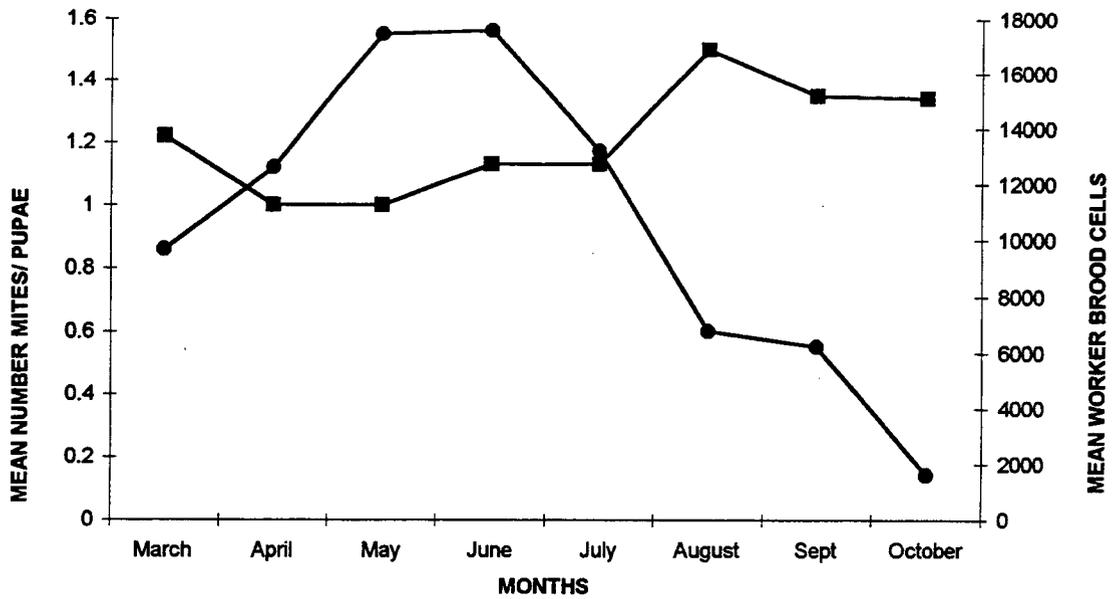
Mite reproduction in the brood cells is a complex process that involves numerous factors related to both mites and bees (Ifantidis, 1988). Female mites prefer drone brood as mentioned earlier; this preference depends neither on the number of infesting mites nor on the absolute number of drone brood cells available in the colony (Fuchs, 1990).

Different strategies are developed by *V. jacobsoni* to reproduce successfully inside the brood cells of *A. mellifera*. Some mites do not reproduce at all while others reproduce immediately upon entering the brood cells (Fuchs, 1994; Fuchs & Langenbach, 1989). However, studies done in tropical areas with Africanized honey bees (*A. m. scutellata*) and hybrids of *A. m. carnica* in Brazil and Uruguay have shown great percentages of infertile female mites in the worker brood cells (Camazine, 1986; De Jong et al. 1984; Ruttner et al. 1984; Rosenkranz and Engels, 1994). This suggests a possible host-parasite adaptation by the tropical *A. mellifera* biotypes, as has been described for the eastern honey bee, *A. cerana*. Here, the parasite-host relationship is stable and the mite causes no apparent damage to the colony because mite reproduction is restricted almost exclusively to drone brood cells (De Jong, 1988; Rosenkranz et al. 1993; Tewarson et al. 1992).

SUMMARY

Based on these results mite load decreases in host worker brood as the number of brood cells increases while in the drone brood host, mite load remains constant.

Many researchers have studied the biology of *V. jacobsoni* as a parasite of *A. mellifera*, but more information on the host-parasite relationship and the distribution of mites inside the brood cells of this non-adapted host is needed to further enhance control measures.



Remarks:

The line with square symbols represents the mean number of female mites per infested pupae over time. The line with circle symbols represents the worker brood host size over time.

Fig. IV. 1. Relationship between mite load (squares) and worker brood (circles) in the colonies.

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CHAPTER V
DRONE DRIFT AS A MECHANISM OF DISPERSAL IN
***VARROA JACOBSONI* OUDEMANS**

ABSTRACT

Drone drift as a mechanism for intercolonial dispersion of the parasitic mite *Varroa jacobsoni* Oudemans was investigated. Twelve colonies were used in this study. These colonies were randomly paired and the drone population in one of each pair was color-marked. Every five days, marked drones that had drifted to the unmarked colony in each pair were collected and the drone drifting rate was determined. Drone drift rate ranged between 5.4% to 85.3%. In a second experiment, six colonies were used to measure mite load on flying drones as they departed the colonies on afternoon mating flights. Mite load from drones exiting the colonies was recorded during a six week period. Over time, mite load per drone increased as the number of flying drones decreased in the colonies. Intercolony movement of *V. jacobsoni* by drifting drones is an important mechanism of transmission in an apiary.

INTRODUCTION

Honey bee drones do not participate in honey production, pollination, brood rearing or colony defense. Their role in the colonial life history is solely to mate with queens (Currie, 1987; Witherell, 1971). Flight activities are performed by drones for the purpose of orientation, mating and defecation (Witherell, 1971). These activities begin when adult drones are about 5-7 days old. The first flights of young drones last a few

minutes and are made for orientation purposes (Oertel, 1956). If weather conditions are suitable, adult drones start flying at noon, with a flight peak between 2-4 p.m. (Ruttner, 1966; Currie, 1987).

Following mating flights, drones will often mistakenly enter other colonies, a process called drifting. Drifting drones may carry diseases or parasites and may play an important role in spreading these organisms between colonies (Bailey, 1958; Butler, 1939; Royce et al. 1991), especially in colonies placed close together as in commercially managed honey bee apiaries. Drifting honey bees are considered to be important in the horizontal transmission of mites among colonies (Free, 1958, Free et al. 1961). Royce et al. (1991) demonstrated that horizontal transmission of tracheal mites among managed colonies occurs mainly through drifting. Drone drift is approximately two to three times as frequent as worker drift (Free, 1958).

The purpose of this research was to investigate the relationship between drone drift and transmission of *V. jacobsoni*, and to evaluate the importance of drifting drones as a mechanism of mite dispersal between colonies.

MATERIALS AND METHODS

Twelve colonies were used in this experiment. All hives had two brood chambers and were arranged in pairs located 30 meters apart, with members of each colony pair situated 2 meters from each other, and with their entrances fully open and facing the same direction (east). All vegetation near the hives was cut short and landmarks were removed. All colonies were equalized regarding the number of bees, brood and food stores and were

randomly paired. Drone populations were marked in one colony of each pair. The total population of painted drones for each of the marked colonies was counted by examining frame by frame in each colony early in the morning prior drone flight. Every 5 days, samples of painted drones that drifted from their parent colonies to the unmarked colony in each pair were collected early in the morning prior to drone flight. The number of drifting drones in each pair were captured, killed and counted (Table V. 1). This trial was conducted from May 5 to June 12, 1995.

In a second experiment, six colonies were randomly selected and used to measure mite load on flying drones as they departed the colonies on afternoon mating flights. Mite load (that is, number of phoretic female mites per adult bees) in drones and workers at the beginning and at the end of the experimental period was estimated (Table V. 2) (Fig V. 1). Drones flying out of the colonies were collected during 20 minute periods and were placed in CO₂ - filled containers plugged with a cotton swab. The drones were examined in the laboratory for phoretic female mites and the number of mites they carried was recorded for six weeks at seven day intervals (Table V. 3) (Fig. V. 2). Hot water was used to dislodge the mite from the adult drone (De Jong et al. 1982). This trial was conducted from June 23 to July 28, 1995. The data were analyzed using the General Linear Model Procedure (SAS System, 1990). A Poisson-Log linear regression model was used to test for mites/drone that had drifted during the six week examination period (Table V. 4).

RESULTS

Table V.1 shows that the percentage of drifting drones ranged from 5.4 to 85.3%, confirming that a high rate of drone drift may occur between adjacent colonies. The total drone drift rate was 35% among all colonies during the five week trial period. This rate of drone drift should be considered a minimum estimate as it measured the drift rate only between adjacent colonies in a paired situation; other drones would have drifted to colonies further away than the pair colony.

Table V. 1. Percentage of drifting drones.

Colony pair	Marked drones (n)	5/23/95	5/28/95	6/2/95	6/7/95	6/12/95	Total drifting
		----- (%) -----					
1-8	260	5.4	17.7	21.0	4.6	0.8	49.6
2-10	453	8.2	9.1	0.4	1.8	0.2	19.6
3-6	112	5.4	4.5	2.7	3.6	0.2	16.9
4-7	161	13.7	14.9	2.5	0.6	1.2	32.9
5-11	150	49.3	24.0	8.0	2.7	1.3	85.3
9-12	55	0	1.8	1.8	1.8	0	5.4
Total	1191	12.8	12.8	6.5	2.5	0.7	35.3

Table V. 2. Mite load for adult workers and drones in the colonies at the beginning and at the end of the experimental period.

----- ¹ Mite load in adult bees-----				
Colony	Workers	Drones	Workers	Drones
	6/23/95	6/23/95	7/28/95	7/28/95
3	0.01	0.02	0.04	0.05
4	0.01	0.03	0.03	0.15
6	0.03	0.16	0.02	0.38
7	0.01	0.03	0.01	0.09
8	0.01	0.03	0.02	0.14
9	0.004	0.03	0.01	0.27
AVG	0.01	0.05	0.02	0.18

¹ Mite load is expressed as the number of adult female mites per adult bee.

Table V. 3. Number of phoretic mites carried by flying drones during the six weeks experimental period.

Week No.	Colony 3		Colony 4		Colony 6		Colony 7		Colony 8		Colony 9	
	Drones	Mites										
I	10	1	16	1	63	1	112	1	13	1	10	1
II	16	1	9	1	46	2	7	1	2	1	23	1
III	6	1	12	1	91	6	11	1	88	1	212	3
IV	28	1	4	1	4	2	2	1	2	1	8	1
V	6	1	1	1	68	1	11	1	69	8	33	1
VI	11	1	7	1	37	1	8	1	2	1	12	1
Total	77	6	49	6	309	13	151	6	176	13	298	8

The data analysis revealed significant differences in the rate of mites/drone in the colonies over time (P-value=0.0001) (Table V. 4) (Fig V. 2). This rate of drone mite load increased as the number of drones decreased in the colonies. No significant statistical differences occurred among colonies in the rate of drone mite load (P-value = 0.649).

Table V. 4. Poisson-log linear regression of mites/drone on drones flying during six weeks experimental period.

Coefficient	Estimate	Standard error	P-value
Intercept	-2.1491	0.2061	0.0001
Drones	-0.0133	0.0032	0.0001

95% CI = (0.9932, 0.9804)

Equation: $\text{Log}(Y) = \beta_0 + \beta_1 \text{drones}$

Median $Y = \exp(-2.1491 - 0.0133 \text{drones})$

DISCUSSION

The data for drifting drones displayed a range from 5.4% to 85.3% between adjacent colonies. Individual colonies displayed great variation in the frequency of drone drifting, which suggests that drones have a marked tendency to drift among colonies. Therefore, there is a continuous risk of mite transmission and re-infestation from drifting drones. Accorti (1991) reported ranges of drifting worker bees from 5% - 70% in colonies of *A. m. ligustica* in Italy. The results presented in this work are in agreement with Free (1958), who did a series of experiments on drifting bees and reported the percentage of drifting workers to be ca. 7.9% versus 41.3% for drifting drones.

Rademacher (1991) observed infestation of *V. jacobsoni* from infested colonies to uninfested colonies introduced to an apiary. According to this author, the degree of infestation increased rapidly in the uninfested colonies over a period of up to six months. She concluded that, within this period of time, colonies which initially had low infestations reached the same level of infestation as their adjacent colonies. Her results suggested that drifting of infested bees contributed to mite population increase.

Duranville et al. (1991) showed that drifting worker bee foragers may carry *V. jacobsoni* from an infested apiary to other apiaries up to 800 m away. Studies done by Sakofski and Koeniger (1988) also reported a significant correlation between the number of drifting bees and the number of transferred mites. However, the number of transferred mites was significantly higher than predicted, suggesting that there may be other factors contributing to inter-colonial mite transmission.

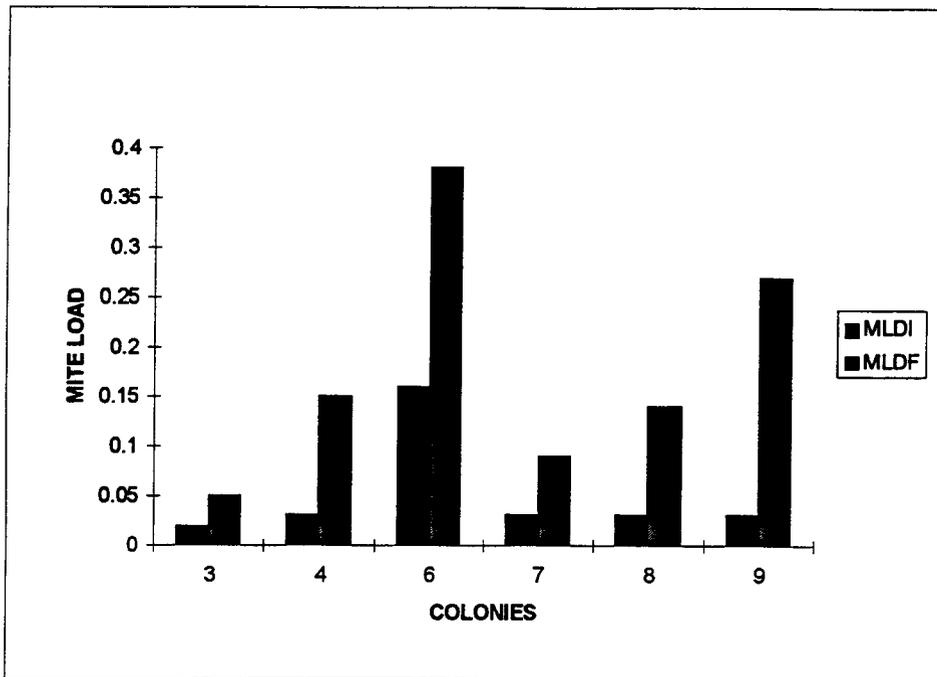
Differences in drone infestation rates among host age groups has been reported (Huttinger et al. 1981). They found great numbers of young drones in the hive to be highly infested with *V. jacobsoni* as compared to flying drones. The mechanism responsible for this drone age preference is still unclear. During the spring, the number of drifting bees entering other colonies was relatively low, but increased at the end of the nectar flow (Sakofski et al. 1990; Sakofski, 1990). This suggests that the risk of mite infestation due to drifting bees is higher when the nectar flow is scarce. Other factors such as robbing may also be important in the increased transfer of mites between colonies, especially when the honey flow is reduced or during periods of low nectar availability since robbing is more likely to occur during this time.

Although the present study was done in colonies with low infestation rates, a trend in number of mites per drones over time was observed. The results from the data analysis showed highly significant differences between the rate of mites per infested drone and the number of flying drones. The data suggest that the mite infestation rate increases as fewer drones are found in colonies. No significant differences in the rate of increase of mites per drone among colonies was observed. According to these results, in late summer and early fall when fewer drones are produced in the colonies, the mite population on adult drones

increases the transmission of mites *via* drifting drones. In addition, because the number of drones in a colony is positively correlated with the colony size (Free, 1957), and workers regulate drone populations by evicting drones in late summer and fall as well as under conditions of severe nectar dearth, increased rates of drone drift and mite inter-colonial transmission should be expected.

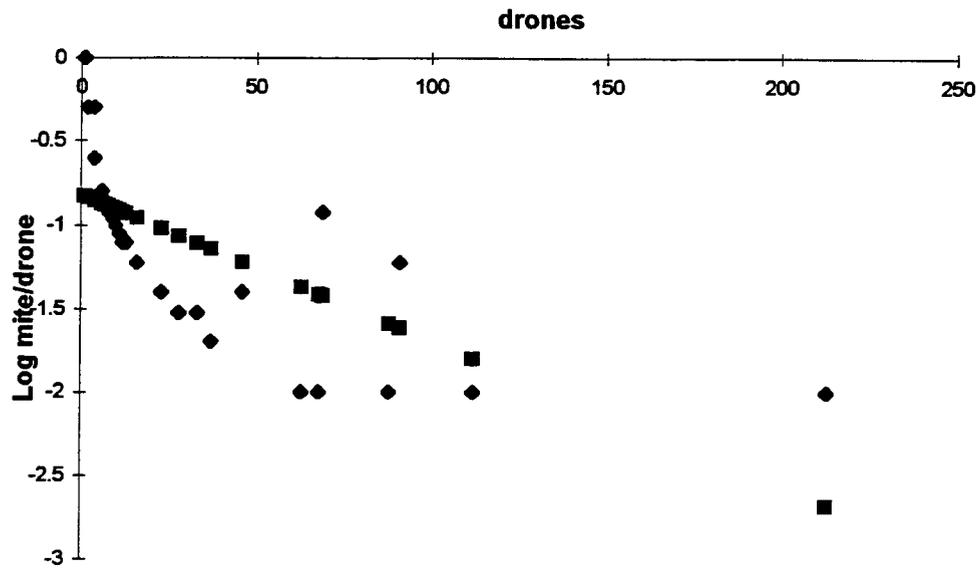
SUMMARY

Based on the knowledge that drones drift at high rate between colonies, and drone mite load increases as the drone population decreases in colonies, the transmission of *V. jacobsoni* by drifting drones is more likely to occur under conditions where the colony is weak, the nectar flow is reduced, and drone population is low. Although this study contributes to the understanding of mite horizontal transmission between colonies, further studies need to be done to elucidate other possible factors that may influence the spread and dispersal of mites in managed apiaries to provide more information for designing suitable integrated control methods.



Remarks: MLDI is the drone mite load at (June 23, 1995)
MLDF represent the mite load in adult drones at (July 28, 1995)
Mite load is expressed as the number of adult female mite per adult drone.

Fig. V. 1. Colony drone mite loads at the beginning and end of the experimental period.



Remarks: Mite load is expressed as the log mite/drone.
Diamonds represents the actual data.
Squares represents the predicted data.

Fig. V. 2. Mite loads for flying drones during six weeks.

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SUMMARY

Varroa jacobsoni Oudemans, a native parasite of *Apis cerana* F. feeds and reproduces almost exclusively in drone brood, causing little damage to the host. When using *Apis mellifera* as a non-adapted host, *V. jacobsoni* reproduces in worker brood but still maintains a strong preference for drone brood. Mite infestation is detrimental to *A. mellifera* colonies due mite's ability to build up population levels rapidly, ultimately resulting in the death of the colonies.

In this study, some aspects of the bionomics of *V. jacobsoni* and of *A. mellifera* were investigated. Evaluations of brood host size and mite infestation rate demonstrated that in worker brood of the host, the infestation rate decreases as the number of brood cells available in the colony increases, whereas in drone brood the infestation rate appears to be constant. This suggests that in cases of severe infestations, mites will disperse among the available cells, keeping the parasitization level at a threshold that may prolong the host colony's survival. It appears that when honey bee brood is infested by a large number of mites, brood rearing may be disrupted to the point that parasite and host populations will decline rapidly, leading to the death of the system.

The importance of drifting drones as a mechanism of mite dispersal between colonies was evaluated. Drones drifted in large numbers between colonies and the number of mites per drone increased when drone population declined. Therefore, incipient varroatosis due to drifting drones is likely to occur especially under colony conditions that lead to a decrease in drone population.

Overwintering mite mortality and its relationship to bee mortality during the winter period was examined. No significant association between mite and bee mortality during the winter period was observed. It appears that factors other than bee death are influencing mite mortality during the winter broodless periods when mite reproduction does not take place.

Mite feeding on adult worker honey bee during summer was investigated. It was concluded that *V. jacobsoni* did feed on adult worker honey bees during the trial period, albeit at low frequency.

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