This is to certify that the

dissertation entitled

THE INTERACTION OF APIS MELLIFERA AND VARROA JACOBSONI POPULATION DYNAMICS IN MICHIGAN: SIMULATION MODELING AND FIELD BIOLOGY

presented by

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has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Entomology

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Date June 13, 1997

THE INTERACTION OF *APIS MELLIFERA* AND *VARROA JACOBSONI* POPULATION DYNAMICS IN MICHIGAN: SIMULATION MODELING AND FIELD BIOLOGY

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology

1997

ABSTRACT

THE INTERACTION OF *APIS MELLIFERA* AND *VARROA JACOBSONI* POPULATION DYNAMICS IN MICHIGAN: SIMULATION MODELING AND FIELD BIOLOGY

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This dissertation was divided into two components, computer simulation and field biology. The computer simulation is interactive and demonstrates the relationship between the life histories of *Varroa jacobsoni* and *Apis mellifera*. The field component studied the development of the mite, its reproductive biology and some diagnostic methods used for detection.

The simulation model was developed using a software package known as Stella II. It generates population statistics at regular intervals throughout a designated time period and outputs diagrams, equations, tables and graphs. The model is designed as a tool that can help a user predict the best time for applying either a biological or chemical control, or help a researcher decide which characteristic trait can have the greatest impact on the mite population.

The field component of this project consisted of an experiment that had four treatments (one control and the other three received 5, 10, and 25 mites, respectively) with five replications. The mite population was monitored every other week from May until October 1994. Two different methods of estimating the population were used; one from mite downfall from sticky board and the other from live bee and brood populations. Over the period of one summer, the mite population increased 81, 188, and 193-fold for the groups that were infected with 25, 10 and 5 mites, respectively, from the sticky board

estimate. Mite population estimates were 2,032, 1,880, and 968 mites for the three groups, respectively, from the sticky board. The mite estimate from the live bee population was always larger than the one obtained from the sticky board. The sticky board method was better than the adult bee and brood samples for the initial detection of mite populations at low infestation levels. In addition, it was found that the mean number of offspring reaching maturity are 1.82 and 2.69 offspring in worker and drone cells, respectively (only the mothers that reproduced males and females were included). In multiple infested cells, the average number of offspring was 1.26 and 2.03, respectively. The study found that 82 and 90% of the mites were fertile in worker and drone cells, respectively.

DEDICATION

To my wife and my sons Zyaid and Rami

Thank you for putting up with me during my study

ACKNOWLEDGMENTS

I wish to thank my major advisor, Roger Hoopingarner. I think I was very lucky to have him for my major professor. When I needed to talk to him he was always available, and I appreciated the effort he made on my behalf. I would also like to thank my guidance committee George Ayers, Stuart Gage, Fred Stehr, and Robert Husband for their guidance during my exams, proposal writing and especially for encouraging me to go and talk to them at any time. A special thanks to Robert Husband for his editing and valuable comment on the first three chapters.

I would like also to than Camazine from Pennsylvania State University and Fries from Sweden University for sending me their model which helped me a lot in my start.

I would like also to thank my graduate student colleagues for their friendship and helping me in editing my writing, specially Becky Gore for her help in the modeling.

Finally, I would like to thank King Saud University for supporting my study in Michigan.

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INTRODUCTION

The mite *Varroa jacobsoni* is a parasite of *Apis mellifera*, and constitutes one of the greatest dangers for modern beekeeping (Griffiths and Bowman, 1981; Boot *et al.*, 1993). The reduction of the beekeepers in the U.S. in the last five years from 211,000 to 125,000 is mainly attributed to the tracheal mite (*Acarapis woodi*) and Varroa mite. Since Varroa now is the major problem, many scientists think the loss of bees in the coming years will be greater.

Comparisons from throughout the world suggest that Varroa genotypes or an interaction of Varroa genotype and the environment produce varied degrees of health problem for colonies. Varroa in Europe was thought to have originated from Ussuria (Ruttner, 1983) and is clearly a problem for European bees. Varroa mites in the US are thought to have spread from South America (Delfinado-Baker and Houck, 1989). This same genotype of Varroa, is believed to have been introduced to South America in 1971 from Japan (De Jong *et al.*, 1982). In Brazil, this mite does not seriously debilitate either African honey bees or European Honey bees in Brazil (Moretto *et al.*, 1991). In Europe, if the population is not controlled, colonies infested with Varroa die in three to four years (Ritter, 1984; Fries, 1991). Deflinado-Baker (1989) suggested a lower virulence of mites from North America compared to mites from Europe on the basis of the hypothesis of South American

origin of mites in the US. However, this has been proven wrong (Page and Kraus, 1995). Initial observations in Michigan agree with Page and Kraus's finding.

More than 174 chemicals have been used or tested for controlling Varroa (Wienands, 1988). Pyrethroid Fluvalinate (Apistan), the most common acaricide that has been used to control Varroa all over the world, is the only one approved for controlling these mites in the United States. Beekeepers are new pesticide users and they are using and misusing the pesticide in the U.S. (Jaycox, 1989). There are reports about Varroa mites developing resistance to Apistan in Italy (Colombo *et al.*, 1993; Lodesani *et al.*, 1995) and the pesticide residues in honey and wax from Apistan and other registered products (Milani, 1994; Hansen and Petersen, 1988; Barbina *et al.*, 1990). Integrated pest management programs have been used for control of Varroa in some countries and show good promise for small scale beekeeping.

This study consist of two parts, one is building a comprehensive model for the life history of the honey bee *Apis mellifera* and the bee mite *Varroa jacobsoni* and their interaction. The second part is the study of the population development for honey bees and Varroa mite and the reproductive biology of the mites in the field.

This dissertation is compilation of four ready-to-be-published papers. The first paper is entitled, "Development of early infestation by the mite *Varroa jacobsoni* in honey bee colonies *Apis mellifera* in Michigan". This paper investigates the population growth of *V. jacobsoni* under Midwest conditions and investigated methods of detecting mite infestation at low rates and correlates these infestations to mite population levels in Michigan honey bee colonies. The second paper is entitled, "A Reproductive biology of *Varroa jacobsoni* in

worker and drone brood of the honey bee *Apis mellifera* L. under Midwest conditions". This paper reported number of offspring produced by Varroa mites in drone and worker cells, number of offspring in single infested cells verses multiple infested cells, fertility rates of Varroa mites in worker and drone cells, percent of female mites that produce males only in worker and drone cells, percent of mother mites that died in the brood cells.

The third paper is entitled, "Modeling of honey bee and mite population dynamics". This paper describes in detail the model building of the life history of the honey bee and Varroa mites using a commercial software package known as Stella II. Also, it shows the interaction between the bees and mite population.

The fourth paper is entitled, "Using model simulations to predict population responses in honey bees and mites by introducing biological control, chemical control, and genetically manipulated character traits into the system". This paper illustrates the importance of modeling in predicting the effect of applying chemical or biological control on mite populations and it helps in defining when the best time in the season to treat. More importantly, it shows how Varroa population dynamics are used as a tool to evaluate the effect of separate resistance traits on the population growth of the mites and it helps to clarify which resistance traits should preferably be selected.

LITERATURE REVIEW

Apis cerana, the Eastern honey bee, was the original host of *Varroa jacobsoni*. Initially discovered on the island of Java by Jacobson in 1904, it was subsequently described by the Dutch zoologist, Oudemans, and named after its discoverer (Oudemans, 1904). The shift of *Varroa jacobsoni* from *Apis cerana* to *Apis mellifera* probably occurred in the 1940's in the U.S.S.R. However, the first reports of this event were published in the 1950s (Schimanuki, 1993). *Varroa jacobsoni* was discovered for the first time in the U.S. in 1987 (Dietz and Hermann, 1988). Currently, the mite is present in more than 85 countries and is considered one of the most serious pests of *A. mellifera* colonies in most of the world (Matheson, 1993, 1994, 1995).

The female mite is a dark red-brown and is almost 1.5 mm in diameter. It is the only common parasite of honey bees that can be seen with the naked eye and identified with a hand lens.

The mite reproduces mainly on drone pupae of *A. cerana* (De Jong, 1988), and on worker pupae of *A. mellifera*, although it prefers the drones. Live mites usually occur inside sealed brood cells or are partly hidden between the abdominal segments of adult bees so, in spite of their size, they are not easily noticed by beekeepers. Dead mites, which fall from adult bees, can be seen fairly readily in debris from the hive floor.

LIFE CYCLE

The previously inseminated reproductive female mites enter a drone or worker brood cell before the honey bee larva (5-days old) in the cell is capped (Tewarson, 1983). They may feed on the larva initially, but they quickly crawl underneath the larva and immerse themselves in the brood food, at least some of which they ingest (De Jong *et al.*, 1982), with only their movable finger-like peritermes (breathing tubes) exposed (Morse and Hooper, 1985). They remain in the brood food, oriented with their ventral side towards the opening of the cell, until the larva eats the food and thereby cleans off and frees the mites. As many as 21 adult female mites may be seen, apparently immobilized, immersed in the brood food in one cell (De Jong *et al.*, 1982). Bradbear (1988) and Tewarson (1983) stated that the greatest number of mites (up to 20) can hatch from a drone cell. When the larva does not eat all the food, the mite is caught and dies (Beetsma, 1983). After the mites are freed, they begin feeding on the haemolymph of the larva and later of the pupal bee (De Jong *et al.*, 1982). Once the *Varroa jacobsoni* female has fed on the bee haemolymph, maturation of the first spermatocyte and fertilization of the first oocyte occurs (Ramirez and Otis, 1986).

The female mite lays the first male egg about 60-64 h after the cell is capped (Martin, 1994; Rehm and Ritter, 1989); the next eggs, usually female, are laid at 30 h intervals. The eggs are laid singly on the cocoon, on the covering of the pupa, or rarely, on the larva or prepupa, or on the wall of the cell (Tewarson, 1983), or between the developing larva and the wall of the cell (Bradbear, 1988; Martin, 1994). One to seven eggs are laid (Martin, 1995). The mite probably feeds for the last time, and oviposition ends, when the worker or drone pupal eyes become dark (for workers, day 18, or hour 216-220 of pupal development;

for drones, day 19 or hour 240 after leaving the first larval instar) (Ifantidis, 1983). If several infective females enter the same brood cell, not all of them necessarily reproduce (Ramirez and Otis, 1986).

A six-legged protonymph hatches from the egg and feeds actively for 48 h after which it molts into an eight-legged deutonymph which also actively feeds on the haemolymph of the pupa. It is similar to the adult mite except for its white color. After about 3 days, the deutonymph molts into an adult which still has a lighter color than the mother mite. The complete development inside the bee cell of the female mite takes 7.5 days and 5.5 days for the male (Ifantidis, 1983), (8-10 for the female and 6-7 for the male; Grobov, 1977; Tewarson, 1983).

The female *V. jacobsoni* mites reach maturity inside the capped brood cell, 24 h after becoming adults (Ifantidis, 1983). By that time the males that moult to adults, approximately 220 h after larval engorging, are probably ready to mate with the females, and they presumably search for the females and mate with them. The male and immature female offspring die shortly after the brood cell is uncapped and the adult bee emerges.

The infective adult female mite, whether fertilized or not, leaves the honey bee cell by phoresy on an emerging bee, or by herself, after which the mite's chelicerae (mouthparts), pierces the intersegmental membranes (or other soft parts) of the bee and feeds on its haemolymph for several days. The mites are phoretic between 1-3 weeks before they enter a cell with a larva (Boot *et al*, 1994), where they feed on the prepupa and begin laying eggs.

IMPACT OF MITE ON BEE POPULATIONS

The mite can impact the bee population in a variety of ways. First, it has a direct impact because it parasitizes the bee. Secondly, it can change the behavior of the adult bee. In addition, it often brings secondary diseases into the bee colony.

Direct impact. Mite infestations shorten the life span of the bee. A summer bee lives for approximately 28 days, whereas a bee infested with two mites during its development may live for only seven days, and if infested with 6 mites dies shortly after hatching (De Jong *et al.*, 1982). Goncalves *et al.* (1985) stated that the mean life span of bees is reduced by half. The life span of the Varroa diseased bee depends on the bee's age when the mite fixes itself on it (Dietz and Hermann, 1988).

When a larva is infested with 1,2,3,4, or 6-8 mites, the loss of weight of the resulting adult is 6.5%, 10%, 11%, 14,% 17% and 25% respectively (Beetsma, 1983). The life expectancy of adult bees is 28, 18, and 9 days when the pupae have been infested with 0, 1, and 2 or more mites (Beetsma, 1983).

Schneider (1986) stated that the number of spermatozoa decreased by 50% when the drone was infested with more than 3 mites. In varroatosis colonies, worker and drone emergence is delayed by 2-4 days (Smirnov, 1978).

Indirect impact. Along with directly shortening the bee's life span, the mite is responsible for carrying pathogens to the bee. It has been determined that the Varroa mites can carry the bacterical pathogens of haffniosis, virus paralysis and nosema diseases (Kutsenko, 1975; Mikitiuk *et al.*, 1975; Sidorov and Stolvov, 1975). Platukhina *et al.* (1975) separated 22 species of micro-organisms from Varroa, of which two are pathogens of bees.

In general, varroa infested bees have 2.2 times greater bacteria in the haemolymph than healthy bees (Smirnov, 1978). Koch and Ritter (1987) could find significantly more bacteria in the haemolymph of adult bees which had been infested with three mites than the uninfected control group or in bees which were infested with only one or two mites.

Smirnov and Kudriavtsev (1977) obtained experimental evidence of the Varroa mites being able to carry the pathogen agent of AFB from diseased to healthy colonies.

Batuev (1979) did laboratory tests where Varroa mites were placed on bees that had been injected with acute paralysis virus (APV). The following day these mites were transferred to healthy test bees. After 20 days only about 9% of the bees were alive, compared with 60% of the control. This virus is relatively common, but it only passes into the haemolymph and attacks vital organs if it can propagate on a massive scale as in the presence of varroatosis (Bailey, 1981). Ball (1985) demonstrated its presence in heavily infested colonies. Bailey and Ball (1991) reported that mites activate the acute paralysis virus when they attack the bees and then transmit it to kill further individuals. It is estimated that varroa can transmit APV from one honey bee pupa to another with an efficiency of about 70% (Wiegers, 1986). Varroa also act as a vector for sacbrood and black queen cell virus. Bailey and Ball (1991) stated that the deformed wings of the adult that are produced from the parasitized pupa is invariably caused by deformed wing virus which is transmitted by mites. Strick and Madel (1988) stated that Hafnia was successfully transmitted from septic infected test pupa to healthy pupa by the mite. The effect of the parasitization depended upon the number of mites that attacked. Seventeen percent of the pupae suffered from septicemia if

one mite attacked, 30.7% for two mites, 81.8% if attacked by four mites; and 95% if attacked by seven mites.

The effect of the pathogen is varied, depending both on the type of pathogen and the amount present. Secondary infections lead to decreases in bee life expectancy (Ritter, 1988), and also to a reduction in both the drive for self-cleaning and the drive to care (Smirnov, 1978).

Impact on the bee colony. Salchenko (1971) observed that infestation levels of mites in bee colonies ranged between 3% and 85% when bees prepared for winter. German research has suggested that a critical limit is 10 mites/day/colony on the bottom sticky sheet. This roughly corresponds to a mite population ranging from 1000 to 1500 mites per colony. In 1989 Jaycox lowered that threshold to three to five mites per day.

It is estimated that if two percent of the worker brood is infested that the population of the hive will be reduced by 1%. Colonies in which 20 mites have been found for every 100 bees in the autumn become very weak. In those in which greater than 50 mites per 100 bees were found, all the bees died. In colonies fed sugar (9-10 kgs) in autumn, all the bees died when the ratio was 10-14 mites per 100 bees (Smirnov, 1975; Nikolski and Evdokimova, 1975). It has been estimated that the critical threshold of mites which cause damage to a normal colony is approximately 5,000 and that bee colonies with mite populations that reach an excess of 10,000 will not survive (Mautz, 1987).

Impact on honey production. Since the mean life expectancy of bees infested with varroa during development is reduced by one half, then it is reasonable to estimate that honey production is also reduced by the same half. If two percent of the worker brood is infested,

the population of the hive will be reduced by one percent, and it may be estimated that this would cause a one percent reduction in honey production (Issa *et al.*, 1985). Woo (1993) also found higher infection rates of 30.0 and 52% corresponded to a 30.65 to 46.0% reduction in honey yields.

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DEVELOPMENT OF THE MITE *VARROA JACOBSONI* IN THE HONEY BEE COLONIES *APIS MELLIFERA* IN MICHIGAN AND COMPARISON OF DIAGNOSTIC METHOD FOR DETECTION OF LOW INFESTATION LEVEL IN THE COLONIES

ABSTRACT

Twenty honey bee colonies were divided into four groups one control and the other three received 5, 10, and 25 mites respectively with five replications for each group. The groups were separated from each other to reduce drifting. The development of the mite infestation was monitored every other week from May until October 1994. Estimation of the different mite populations were based on daily mite downfall, or a sample of 100adult bees, and 100 worker and 100 drone broods and estimate of number of adult bees and brood cells.

Over the period of one summer, the mite population increased 81, 188, and 193-fold for the group that were infected with 25, 10 and 5 mites respectively. Based on the daily mite downfall, the population estimates were 2,032 ,1,880 and 968 mites for the groups that started with 25, 10, and 5 mites respectively. The mite estimate from the live bee population was larger than mite estimate obtained from sticky board. However, variation in mite populations between the colonies was large. The sticky board method was better than adult bees and brood samples for the initial detection of mite population at low infestation level.

INTRODUCTION

The mite *Varroa jacobsoni* Oudemans (Acari: Mesostigmata) is a parasite of the honey bees *Apis cerana* and *Apis mellifera*. It is present in more than 85 countries and is currently considered one of the most serious pests of *A. mellifera* colonies in most of the world (Matheson, 1993, 1994, 1995). There are a number of factors that effect the reproductive rate of the mite. Reproduction occurs in sealed honey bee brood cells. Hence, mite population growth occurs only in the presence of brood cells. Other factors include host-specific effects of the bee (Moritz and Hanel, 1984; Buchler, 1990; Rosenkranz *et al.* 1990; Fuchs, 1991; Moretto *et al.*, 1991b; Otten, 1991; Kulincevic *et al.*, 1992), geographic and climatic factors (De Jong *et al.*, 1984; Moretto *et al.*, 1991) and possibly Varroa genotypes (Delfinado-Baker and Houck, 1989; Guzman *et al.*, 1996).

In the Mediterranean climate of California the initial population is capable of increasing 300-fold during one year (Kraus and Page, 1995). In colder, temperate climates the increase averages about 10-fold per year (Ritter, 1984; Fries *et al.*, 1991b; Korpela *et al.*, 1992); but can increase up to 100-fold within one summer (Fries *et al.*, 1991). In tropical climates the parasite seems to be less virulent (Ritter and De Jong, 1984). In sub-tropical climates the infestation rate is lower than in temperate climates (Moretto *et al.*, 1991b). If the population is not controlled, colonies infested with *V. jacobsoni* die in three to four years (Ritter, 1984).

An important part of control is the initial detection of the mite. Early detection with low infestation rates is important in bee colony management. Ritter (1981) and De Jong (1984) suggest the following diagnostic method: count mites that fall from the bee due to natural causes, examine bee samples for phoretic mites, check capped brood samples for mites

while they are reproducing, and treat the colony with acaricides. For low infestation levels (below ten mites), the use of acaricides may be the only effective method for detecting the mite with acceptable levels of precision in broodless colonies (Ritter, 1984). If the mite population is between ten and 100, then the examination of hive debris should allow for detection (Ritter, 1984). In fact, Ritter reported that live bee or brood examinations are insufficient for population levels below 100 mites per colony (1985). Liebig *et al.* (1984) reported a close correlation between mites collected in hive debris and the size of the Varroa mite population. Fries *et al.* (1991a) also compared different diagnostic methods for detection of low Varroa mite infestation levels. They concluded that debris was more effective than examining the brood itself for low infestation rates. They said it was preferable to other methods because of its simplicity and efficacy.

The objective of this research project was to investigate the population growth of *Varroa jacobsoni* under Midwest conditions and investigate methods of detecting mite infestations at low rates and correlate it to mite population levels in Michigan honey bee colonies. Initial observation suggested that the impact might be greater on bee colonies in Michigan than in Europe. Delfinado-Baker and Hauch (1989) suggested that the European mite has lower virulence based on the hypothesis that the mite originated in South America.

MATERIALS AND METHODS

Twenty packages of bees (0.9k of bees per package) were separated into four groups, each containing five colonies. They were installed into single chamber Langstroth hives containing honey and comb foundation on the first of May in East Lansing, Michigan. Each colony was treated with two Apistan strips (10% fluvalinate). The four groups were placed

in separate locations on the Michigan State University campus in an effort to reduce drifting between groups. Robbing screens also were used (Hoopingarner, 1982). All groups were managed optimally as for honey production and were treated with Fumidil B (Mid-Con) in May and treated with terramycin antibiotic (Pfizer) in May and July. One group was the control (0 mites), and the other three were inoculated with 5, 10 and 25 mites, respectively. The mites were removed from their host bees using CO_2, collected in small tubes and introduced directly upon the bees on May 15. The experiment lasted about 30 weeks.

Total mite population was estimated using both live bees and hive debris. Live bee estimates were taken every two weeks, beginning May 29th. Between 100 and 200 live adult bees were taken from brood combs and stored in a deep freezer. The mites were separated from the bees by vigorously shaking the bees in 70% ethanol for 3 to 4 minutes. The mites were washed from the bees using a hand-shower over a double wire screen. Number of bees and mites were counted to determine the level of infestation on adult bees, data were adjusted to present number of mites per 100 bees. In addition, samples of 100 sealed worker and 100 drone brood cells were examined when brood was present. The cells were opened and the number of adult females in the cells and on the bees were counted. The amount of brood in the colonies was estimated in each colony using the double-sampling technique described by Roger *et al.* (1983). The bee population was estimated as described by Burgett and Burikam (1985).

The hive debris was collected weekly on a paper sheet placed on the bottom of the hive to monitor the natural mortality. A wire screen prevented bees from gaining access to debris (Ritter, 1981), and a plastic sheet was smeared with cooking oil to catch the mites.

Sheets were left in the hive for three days, and adult females were counted directly on the paper. This was done over a 30 weeks period.

Total number of mites in each colony with brood was estimated by Fries *et al.* (1991b) using the following two methods: (1) daily downfall: average daily mite downfall x 120 (Liebig *et al.*, 1984); and (2) live bees: the infestation rate of live bees x number of bees + infestation rate of brood x number of brood cells (Fuchs and Koeniger, 1984, 1996).

RESULTS

Although the experiment started with four treatments, the control colonies were lost in the first week because of contamination by an infested swarm. One week after the start of the experiment, one sticky board had 60 mites, the nearest one to that had 16 mites. The other three sticky boards were without mites. The colony with 60 mites had 80 mites on the sticky board and 59% adult infestation in November. The other colonies in this treatment group gradually became infested also. Two of the five colonies survived the winter, and both of them had peak mite downfall of 20 and 30 on the sticky board in September, respectively, and they entered the winter with an 18 and 22% adult bee infestation rate. Therefore, only the three other treatments were analyzed. They included those inoculated with 5, 10, or 25 mites.

The entire five colonies that were inoculated with 25 mites were lost during the winter. Their deaths could not be attributed completely to *Varroa*, but may be also due to the cold winter. The maximum number of mites recovered from the sticky board was recorded on the September 17th sampling date. The number of dead mites ranged from 40 to 63 and the adult infestation was between 24 to 34%.

Four of the five colonies that were inoculated with 10 mites survived the winter. The colony that died did not have any more mites than the colonies that survived. The range of mites recovered from sticky boards on September 24 ranged from 25 to 71. The number found in the dead colony was 65 and had 28% infestation of the adults in November. Three of the five colonies that were inoculated with 5 mites died. Once again, there were no differences in the number of mites recovered on the sticky board among the colonies. The two that survived had 26 and 29 mites on the sticky board in September, while the three that died had 18, 25, and 62 mites on their boards and entered the winter with 14, 17 and 21% adult bee infestation rate. Two of the colonies that died had more foulbrood infection than the rest, although they received the same medication treatments in May and July as the other colonies.

Using the sticky board method of calculating mite density (Figure 1), choosing the same dates when live bee samples were taken, the population ranged from 1640 to 2520 mites, with an average of 2,032 in the 25 mite inoculated treatment. The 10 mite inoculated treatment had a smaller peak, ranging from 1,200 to 2,200, with an average of 1,880 mites. The last treatment (5 mites) had an average of 968 mites, with a range from 520 to 1,480.

The mite estimate from the live bee population (Figure 2) was larger than the mite estimate obtained from sticky board counts for all treatments. It averaged 1760 (range 578-2,375), 2,247 (range 1,347-2,775), and 3,119 (range 2,130-3,834), for the 5, 10, and 25 mite treatments, respectively.

Over the period of one summer, the mite population increased 193, 188, and 81-fold for the groups that were infected with 5, 10 and 25 mites respectively, when using the sticky board method of estimating mite population. This was an average of 154-fold increase. When

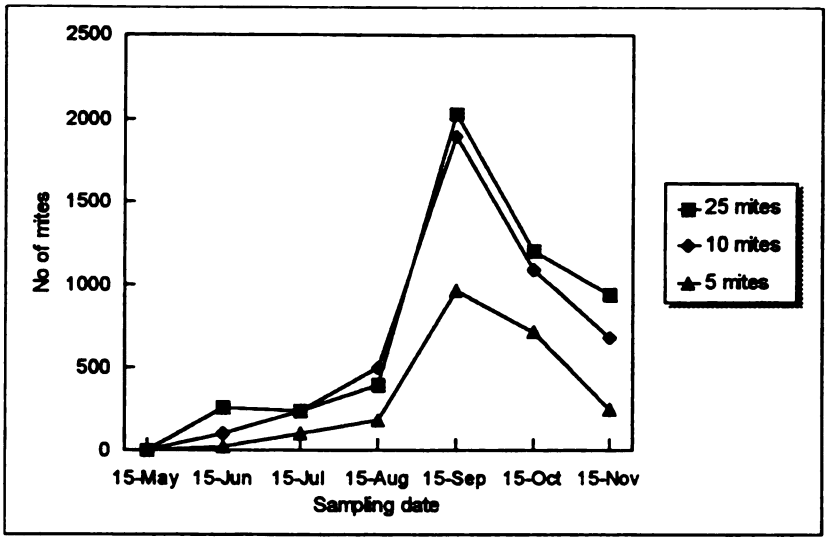

Figure 1. Average number of varroa mites per treatment group (5, 10, 25 mites in initial inoculation), calculation based on average daily mite downfall (x 120, Liebig et al., 1984). The last sampling date estimate has no brood in the colonies.

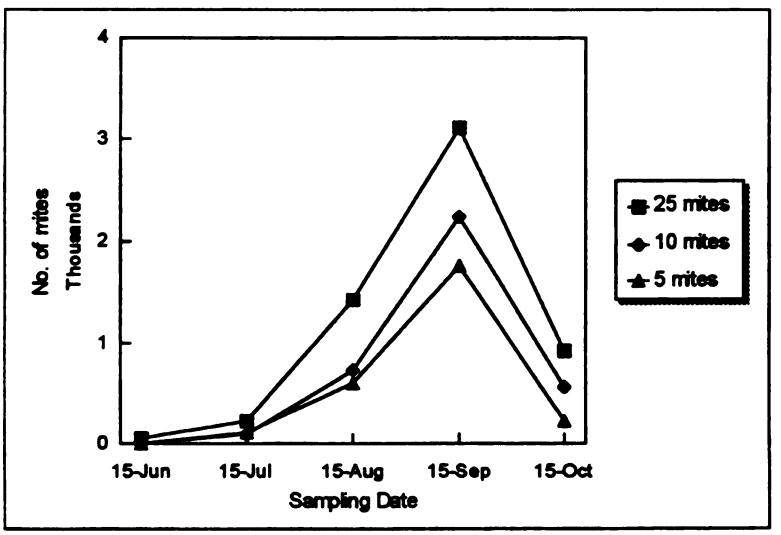

Figure 2. Average number of varroa mites per treatment group (5, 10, 25 mites in initial inoculation), calculation based on number of mites per live bee * number of bees + number of mites per brood cell * number of brood cells. Samples on 15th of October from adult bees only.

estimating the population from the live bee method, there was a 352, 225, and 125-fold increase, respectively. This method had an average increase of 234-fold.

The colonies that did survive the winter were weak the following spring and only covered one or two combs and they had an average of 50% brood infestation rate on May 15. Attempts were made to strengthen these colonies so they could be utilized for other experiments, but they were unsuccessful. All of the colonies collapsed in September.

The number of mites found on the sticky boards (Figure, 3) increased slowly until the middle of August for all three treatments. In the middle of August there was a sharp increase in the number of mites found on all the sticky boards. This increase peaked on September 17th for the 10 and 25 mite inoculated colonies. This peak plateaued for two weeks and then gradually declined until the population started to increase in March and April. For the third treatment (colonies inoculated with 5 mites), the downfall began to sharply increase at the end of August similarly to the other two treatments. It sharply increased until the 17th of September (where the other two treatments peaked), but continued to increase until the 7th of October. This group did not experience a plateau, but declined immediately, until the downfall increased in March and April when the bee colony began its brood rearing.

The infestation rate on the adult and brood population (Figures 4, 5, 6), increased drastically when the brood and adult population declined at the end of the season. In general, the trend in these graphs are in agreement with the results from natural death rate. The level of infestation on adult bees (Figure 4) ranged from 0.3 to 3% the majority of the summer and was the highest on wintering bees at the end of November when there was no brood and the bee population was low. The adult infestation rate varied widely between colonies within the same group. For example, in November there were between 25 to 34%, 13-28% and 7-17%

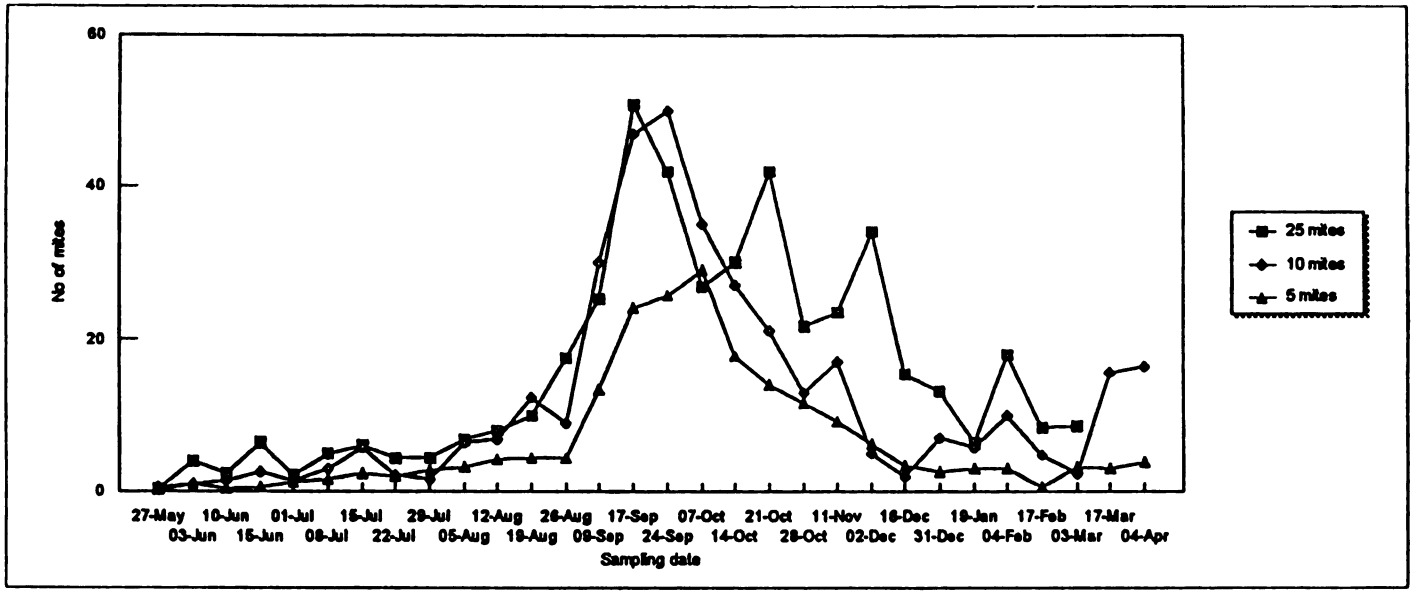

Figure 3. Average number of dead varroa mites per treatment group (5, 10, 25 mites in initial inoculation) per three days collected on the sticky board.

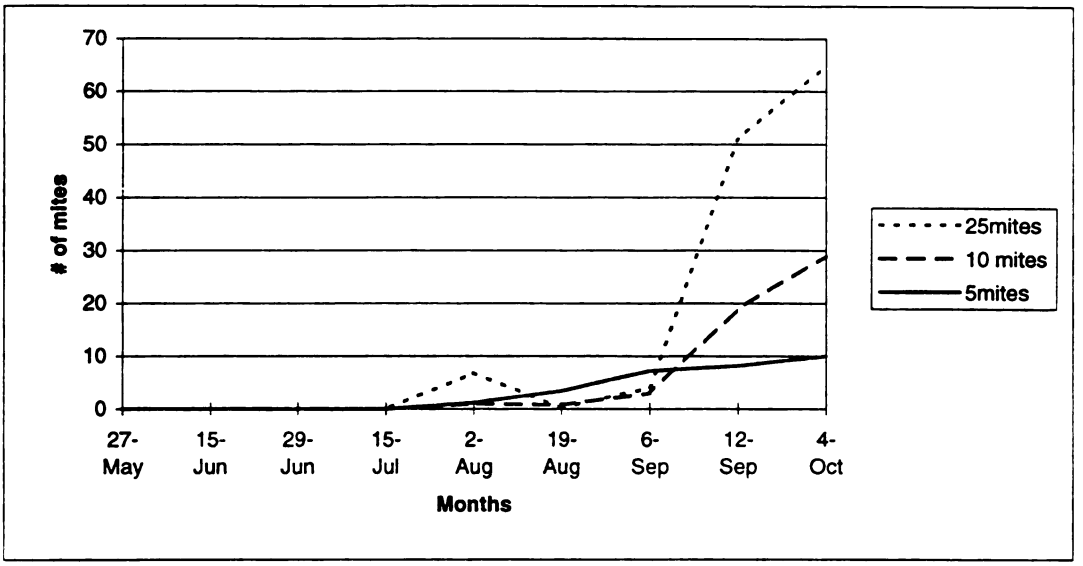

Figure 4. Average number of mites per 100 worker cells per treatment per group (5, 10, 25 mites in initial inoculation)

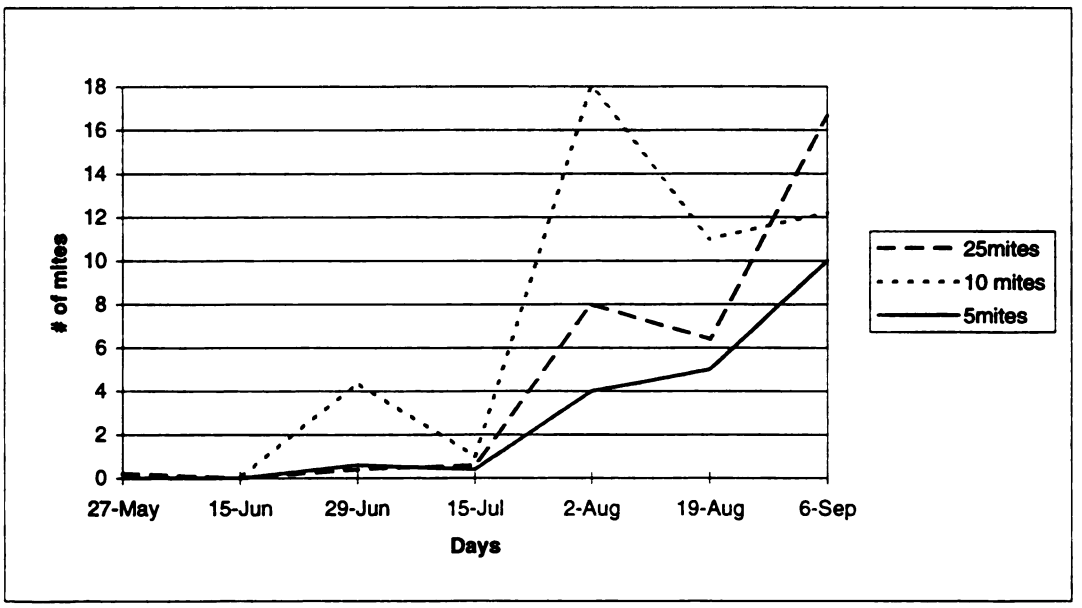

Figure 5. Average number of mites per 100 drone cells per treatment group (5, 10, 25 mites in initial inoculation)

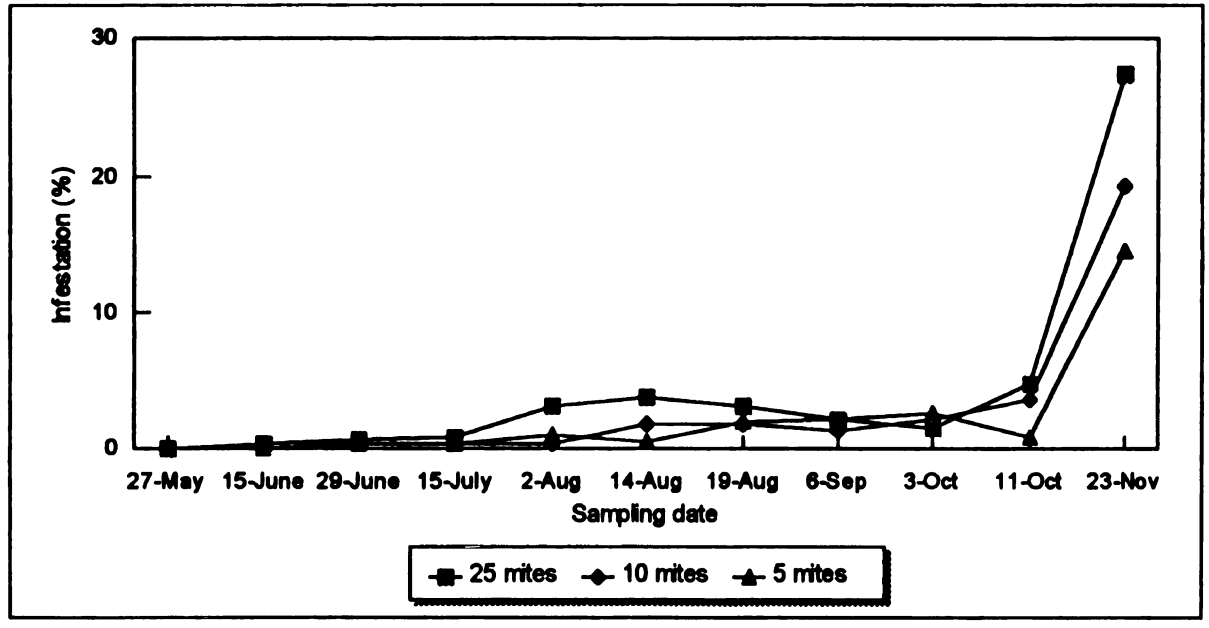

Figure 6. The percentage of adult bees infested by varroa mites per treatment group (5, 10, 25 mites in initial inoculation).

for groups one, two and three, respectively. Also wide variation occurred in the number of mites in worker and drone cells, e.g., the number of mites ranged between 30 -200 mites per 100 worker cells in group one on October 4th.

One of the objectives of this study was to compare the two methods for estimating the mite population. The sticky board method is statistically better for the initial detection of mite populations at low infestation levels ($p<0.001$, Colton, 1974). For example, on the first sampling date (15 June), the sticky board detected mites in 12 of the 15 colonies while the adult and brood population detected mites only 2 out of 15 times. When populations grew, by 15 July, the sticky board detected mites in all 15 colonies, whereas the live adult and brood population detected mites in 9 of the 15 colonies. Once the population grew even larger by 15 August, both methods detected mites in all the colonies. This continued on 15 September. Then, on 15 October, the live bees and brood population detected mites in 13 of the 15 colonies, while the sticky board tested positive in all 15 colonies. Although the sticky board had a higher rate of detection (100%), the two methods were not statistically different from each other on October sampling date ($p<0.171$). When there was no brood present, there was no significant difference between sticky board and sampling of live bees.

The next question concerned the differences between examining the bee brood vs. the adult bee population. Neither one was good at detecting mite populations at low levels. On all five dates, there was not a significant difference between the two groups ($p=0.1710$, 0.4032, 0.7941, 1.0, 0.1710, respectively).

Correlating the relationship between the live bee samples and sticky board samples, it was found that all the correlations were positive, except for some correlations with the

drone brood. The best correlation was between the sticky board and worker brood (0.79 in all treatments, Table 1).

Along with the correlations, the data were fit to a series of linear regression models. It was found that the number of mites recovered on the sticky board could be explained by the following linear regression (r^2=0.656, $p<0.001$):

$$TMS = 199.8 + 0.242*AB + 0.682*WB - 9.467*DB$$

where:

TMS = total mites on sticky board
AB = mites found on adult bees
WB = mites found in worker brood
DB = drone brood

Since the p-value associated with the constant and adult bees and worker brood were almost significant ($p<= 0.053$) while the p-value associated with the drone brood was not ($p<0.341$), the model was revised to exclude the drone brood from the estimate. When the drone brood is removed, the r^2 is still significant (r^2=0.518, $p<0.001$), and the equation is as follows:

$$TMS = 282.449 + 0.348*AB + 0.594*WB$$

where:

TMS = total mites on sticky board
AB = mites found on adult bees
WB = mites found in worker brood

The p-value associated with each of these coefficients was highly significant ($p<0.005$). The number of mites found in the worker brood alone was the best single predictor of number of mites on the sticky board. This factor explained 46% of the variability in sticky board numbers (p-value < 0.001). Figures 7 and figure 8 show the brood and bee population, respectively.

Table 1. Comparison between different sampling methods for detection of *Varroa jacobsoni* at different infestation levels, including their correlation coefficient (r) and the associated level of significance (p).

Sampling method	r				p			
	5	10	25	all tmt	5	10	25	all tmt
Sticky board v. adult bees[1]	0.74	0.370	0.320	0.40	0.001	0.111	0.176	0.002
Sticky board v. live bees	0.73	0.830	0.810	0.77	0.001	0.001	0.001	0.001
Live bees[4] v. adult bees	0.90	0.750	0.650	0.74	0.001	0.001	0.002	0.001
Sticky board v. worker brood	0.48	0.910	0.850	0.79	0.033	0.001	0.001	0.001
Mites in worker v. adult bees	0.47	0.440	0.250		0.036	0.053	0.290	
Sticky board v. drone brood	-0.13	-0.210	-0.320	-0.14	0.610	0.380	0.210	0.290
Mite in worker v. mite in drone	-0.24	-0.160	-0.260		0.350	0.490	0.310	
Live bees v. adult bees[2]	0.89	0.740	0.590		0.001	0.001	0.013	
Live bees v. drone brood	-0.30	0.066	0.690		0.240	0.780	0.002	
Adult bees v. drone brood	-0.26	-0.050	0.096		0.300	0.830	0.710	
Sticky board v. adult bees[3]				0.51				0.050

[1]Brood present.
[2]Only when drone present.
[3]No brood present.
[4]Live bees are both brood and adults.

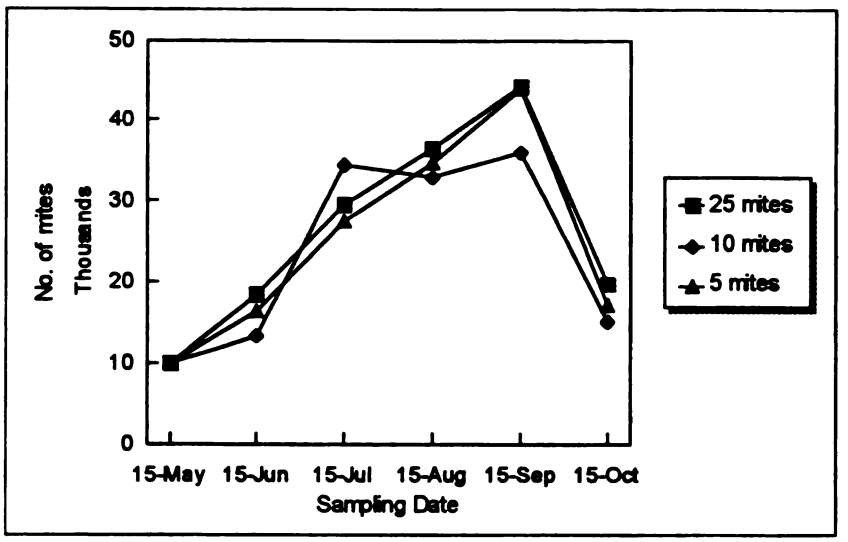

Figure 7. The average bee population per treatment group (5, 10, 25 mites in initial inoculation).

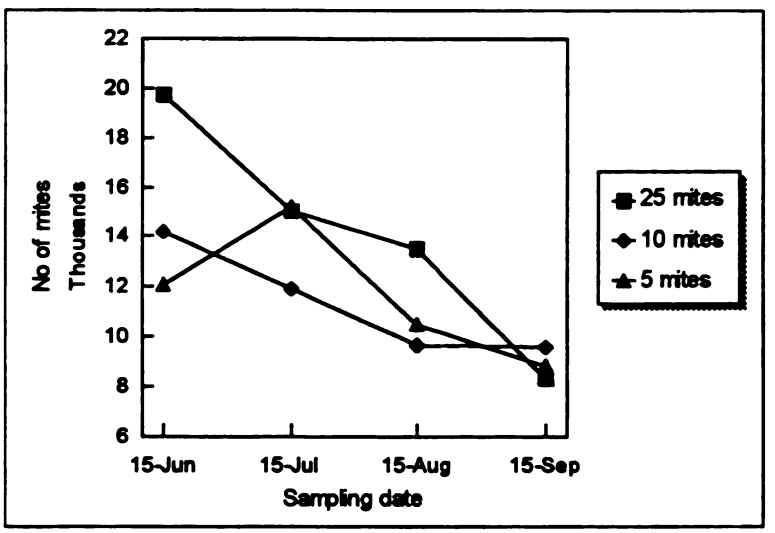

Figure 8. The average total brood population per treatment group (5, 10, 25 mites in initial inoculation).

DISCUSSION

When mite population estimates were based on the natural mite downfall in the hive debries the data show that the mite population can increase an average of 154-fold during one summer. Fries *et al.* (1991b) reported that mite populations could increase more than 100-fold within one summer in a cold climate very similar to Michigan with beginning inoculation levels of five to eight mites. When examining the data from the group inoculated with five mites in the beginning of the experiment it noted that the mite population increased at least 50 times faster than in the Fries *et al.* study. This difference maybe due to immigration of mites from outside the experimental unit despite precautions taken to avoid such a situation. This also may explain the large variation between the colonies within the group. Greatti *et al.* (1992) found daily reinfestation rates in high density honey bee areas of up to 100 mites/colony. Imdore and Kilchenmann (1991) estimated between 3000 - 4000 mites/colony were transported by robber bees when they attacked dying colonies in a neighboring apiary in June.

The estimate from the live bees, adults and broods, yielded a higher and more variable population level than those obtained from the natural mite fall in the hive debris, and this was in agreement with Liebig (1996) and Fries *et al.* (1991a). That probably was due to the noticeably wide variation in infestation between the colonies in the same group, between the combs within a colony and between cells within one comb where a few cells would have no mites and the next would have several mites. This observation was in agreement with others. Rosenkranz *et al.* (1984) and Fuchs (1985) reported that infestation within a single colony varies from one brood comb to another and even from one area of the comb to another. Also the infestation of the adult bees vary from one comb to another (Pappas and Thrasyvoulou,

1986). Liebig (1996) reported live bee estimates are more likely to be affected by the part of the hive from which the sample has been taken. Ellis and Baxendale (1994) stated that the distribution of mites among adult bees and brood are probably affecting the results of the sampling method. Both Fries *et al.* (1991) and Liebig (1996) suggested that the natural mite downfall is more reliable for estimating incidence of Varroa.

Colony-mite population was highest in September and that was possible because brood production was high in August and relatively high in the first two weeks of September at the same time the mite population became high. The brood production was highest in June and July but the mite population was small. The sharp increase from mid August to mid September also could be a result of immigration, if that had an effect, although it has been reported that in isolated apiary after removing the Apistan strips in August, which were in the hives for 65 days, the mites increased to about 1,700 within 122 days (Delaplane and Hood, in press).

The sticky board is the most reliable method for detecting mite infestations when the population is low. In fact, at no time in the study did the live bee and brood estimates surpass the sticky board as a superior method of detecting mite populations. Detection rates from the sticky board were either greater or equal to those occurring from the examination of live bee populations. As the mite population grew, the live bee results became closer to the mite downfall results. This concurs with Fries *et al.* (1991a). Therefore, it is recommended that beekeepers use the sticky board to detect initial populations.

Although the examination of the worker and drone brood was not as good a method of detecting mites as examining mite downfall from the sticky board, especially at low population levels, the number of mites found in the worker brood was highly correlated to the

mite downfall (r = 0.79). It also was significant in both the multiple regression and the simple linear regression model (r^2 = 0.656 and r^2 = 0.460, respectively). This is in agreement with the findings of Boot *et al.*(1995) when he reported that an18% of the mites introduced into a colony were found in the sticky board when bees emerged from brood cells. The correlation with drone brood was negative (-0.14). This was probably due to the small number of drone cells available for the mites.

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REPRODUCTIVE BIOLOGY OF *VARROA JACOBSONI* IN WORKER AND DRONE BROOD OF THE HONEY BEE *APIS MELLIFERA* UNDER MIDWEST CONDITIONS

ABSTRACT

The reproductive biology of the mite *Varroa jacobsoni* Oudemans was studied from June 30 to October 15, 1995 under Midwestern conditions in *Apis mellifera* colonies that were highly infested from the previous year. A total of 353 worker cells containing 697 mother mites and 192 drone cells containing 498 mother mites were found in 959 worker cells and 344 drone cells that were examined. Number of offspring were calculated two different ways, one included infestations that did not produce offspring, or produced male only offspring, and included dead offspring. The second method that is presented in some of the literature excluded these infestations. In an effort to compare this study with studies available in the literature, both methods are presented. It was found that the mean number of female offspring reaching maturity before the bee emerged in worker and drone cells containing a single mother mite are 1.41 and 2.47 offspring respectively, when non-reproduction and male only reproduction were included in the average. When these components were excluded the number increased to 1.82 for workers and 2.69 for drones. In multiple infested cells, the average number of offspring was 1.09 for workers and 1.87 for drones, when non-

reproduction and male only reproduction were included. These increased to 1.26 and 2.03, respectively, when non-reproduction and male only reproduction were excluded. This study found that 86.75 and 93% of the mites were fertile in worker and drone cells, respectively, when including those mother mites that produced male only offspring. When excluding these offspring, the fertility rate decreased to 82 and 90%, respectively, in worker and drone cells. The percentage of female mites that did not produce eggs are 11 and 7% in worker and drone cells, respectively. In addition, mortality of mother mites accounted for 2.29 and 2.7% of the total infested mites in worker and drone cells, respectively.

INTRODUCTION

The mite *Varroa jacobsoni* (Acari: Mesostigmata) is a parasite of the honey bee (*Apis mellifera*) and is currently considered one of the most serious pests of *A. mellifera* colonies in most of the world. On its natural host, *A. cerana* Fabr., the Varroa mite population is generally under the damage threshold because the mite parasitizes primarily drone brood (Konger *et al.*, 1981; De Jong, 1988; Tewarson *et al.*, 1992; Rosenkranz *et al.*, 1993) and *A. cerana* has developed methods to protect itself such as a more efficient grooming behavior (Peng *et al.*, 1987) and its ability to remove parasitized worker brood (Rather and Drescher, 1980; Boecking, 1992).

The mite behaves differently in *A. mellifera* than it does in *A. cerana* colonies. It regularly enters both worker and drone brood, but has a higher fertility and fecundity rate in the drone brood. The number of viable female offspring produced by invading mother mites depends, in part, upon the type of cell the mite enters, whether it is drone or worker; and the

number of invading mother mites per cell. The number of mites entering a brood cell is inversely proportional to the number of offspring produced per female mite.

There is a wide variation in the fertility rate of mites reported among different countries (Ritter and De Jong, 1984; Ruttner *et al.*, 1984; Ifantidis, 1984; Thrybom and Fries, 1991; Camazine, 1986; Sulimanovic *et al.*, 1981; and Rezenkran, 1994). In addition, there is also variation in the fecundity rate (Shulz, 1984; Fuchs and Langenbach, 1989; Ifantidis, 1984, 1990; Engels *et al.*, 1986; and Martin, 1994, 1995).

Without control, the mite population can breakdown a colony in Michigan in one to one and a half years. In Europe the breakdown is much slower, occurring within three to four years (Rosenkranz and Engles, 1985).

The objective of this study was to record the reproduction, fecundity and fertility of Varroa under Michigan conditions and compare these findings with results from other countries.

MATERIALS AND METHODS

Ten colonies of *Apis mellifera* were used in this research. The site was located in East Lansing, Michigan. The colonies were highly infested with Varroa from the previous year and were kept in three story Langstroth hives. Two weeks before the beginning of the study, attempts were made to strengthen and equalize the colonies used. None of the colonies examined had previously been exposed to chemical acaricides.

A total of 959 worker and 344 drone cells were examined on four different occasions from June 30 to October 15, 1995. Two frames from each colony were removed on each sampling day and the contents of at least 30 infested cells were recorded. This procedure was

repeated monthly for four consecutive months. Some of the colonies died during the study and were replaced. In order to estimate the average fecundity of the mites, both worker and drone brood cells were examined. When possible, only those cells containing adult bees that were near emerging were used. If this was not feasible, pupae with dark eyes and light brown thorax were counted (<230 and 322 hours post-capping for workers and drones, respectively). Slightly younger pupae were used for the fertility estimation.

The procedures used for examining and recording the data were the same procedures used by Ifantidis (1990) and are summarized as follows: worker and drone brood cells were examined in cells that contained emerging adults while they were in the process of emerging, the number of Varroa female adults, as well as the number of skins of the last molt of young females, were counted. In addition, the number of adult male(s) and developing mites were also recorded (to use in case there was a question concerning the number of skins present). The number of original mother mites found in the cell was determined to be the number of female adults present minus the number of skins from female deutochrysalis. By dividing the number of skins by the number of original mother mites one finds the average number of offspring produced per mite in the cell.

The examined brood combs were not put in the refrigerator before the examination of their infested cells. Some of the characteristics of reproduction per cycle that were recorded and analyzed included: (1) total number of offspring per producing mother mite; (2) the fraction of mother mites without offspring; (3) the fraction of mother mites with only male offspring; and (4) the fraction of mother mites that were dead in the cells.

Reproduction was calculated using single mite infested brood cells. Some cells containing old pupae are included in the data. The presence of *V. jacobsoni* eggs, proto- or

deutonymphs, confirmed that the female mites were reproducing. The total number of offspring per mother was calculated using two methods. One included mother mites that did not produce offspring and the other included only mother mites that produced viable offspring. Both methods are published in the literature and were utilized here because one of the objectives of this research was to compare mite behavior in Michigan colonies with data already published.

RESULTS

The total number of worker cells examined was 959, from 20 brood combs. Of these cells, 353 worker cells were infested with 697 mites. From the four sampling dates, the infestation rates were 40% in June, 50% in July, 52% in August and 67% in October. Reproduction rates averaged 86.8% in worker cells when including male only reproduction and averaged 82.0% when excluding male only (Table 1). The percent of cells that contained only male offspring averaged 5.1% in worker cells. The number of offspring per mother mite averaged 1.41 when including mites that produced only males and dead female mother mites using single infested cells. The fecundity rate rose to 1.82 when excluding these worker brood cells from single infested cells (Table 2). The average number of offspring decreased to 1.09 when the whole mother mite population was included, regardless of the number of mother mites infesting the worker brood cell when including male only and dead mother mites. The average number of offspring rose to 1.26 when excluding these mites.

There were 192 drone cells from 11 brood combs. These contained 498 mother mites. Infestation rates for the drone brood were 45% in June, 71% in August and 90% in September. Reproduction rates averaged 93.0% in drone cells when including male only

Table 1. *Varroa jacobsoni* reproduction in *Apis mellifera* worker cells under Michigan conditions.

DATE	N	Reproduction (Males present)		Reproduction (Excluding males)		No Reproduction		Male Only		Dead	
		n	%	n	%	n	%	n	%	n	%
6/30/95	53	46	86.8	44	83.0	7	13.2	2	3.8	0	0.0
7/22/95	76	67	88.2	63	82.9	7	9.2	4	5.3	2	2.6
9/15/95	75	66	88.0	60	80.0	8	10.7	6	8.0	2	2.5
10/15/95	51	43	84.3	42	82.4	6	11.8	1	2.0	2	3.9
Average			86.8		82.0		11.0		5.1		2.3

Table 2. Number of daughter mites produced per *Varroa jacobsoni* mother mites in worker brood under Michigan conditions.

Date	All mother mites (including those producing only males and dead mites, excluding those producing only immatures)				Mother mites that produce female offspring (excluding those producing only males, dead mites and immatures)			
	Single infested cells		Total mite population		Single infested cells		Total mite population	
	n	offspring	n	offspring	n	offspring	n	offspring
6/30/95	46	1.46	105	1.04	37	1.81	93	1.11
7/22/95	68	1.47	130	1.16	55	1.82	112	1.31
9/15/95	69	1.41	128	1.22	53	1.83	106	1.38
10/15/95	31	1.29	68	0.93	22	1.81	53	1.25
Average		1.41		1.09		1.82		1.26

reproduction and declined to 89.9% when excluding male only reproduction (Table 3). The percent of cells that contained only male offspring in drone brood averaged 2.3% in worker cells. The number of offspring per mother mite averaged 2.47 in single infested cells that including male only and dead mites and increased to 2.79 offspring when excluding male only and dead from the average (Table 4). The average number of offspring decreased to 1.87 and 2.03, respectively, when the whole mother mite population was included, regardless of the number of mother mites infesting the drone brood cell.

Comparing worker and drone fertility and fecundity data, it was found that drone fertility was higher than worker (93 to 86.8%, respectively). There were more brood cells containing only males in worker cells as compared to drone cells (5.1 to 2.3%, respectively). The mite fecundity rate was also higher in drone cells than in worker cells (2.03 to 1.26 average number of offspring when the whole mite mother mite population was included, respectively).

The rate of decrease in mite fecundity is illustrated in Figure 1 for both worker and drone cells. The graph was generated from the offspring data that excluded male only, dead mites, and immatures). The logarithmic equations are as follows:

$Y = -1.423*\log(x) + 2.523$ for mites infesting worker cells

$Y = -1.196*\log(x) + 1.486$ for mites infesting drone cells

where:

Y = expected offspring
x = number of mother mites in brood cell

The worker and drone models had r^2 values of 0.751 and 0.836, respectively. The data generating the model demonstrated the negative correlation between number of infesting

Table 3. *Varroa jacobsoni* reproduction in *Apis mellifera* drone cells under Michigan conditions.

DATE	N	Reproduction (Males present)		Reproduction (Excluding males)		No Reproduction		Male Only		Dead	
		n	%	n	%	n	%	n	%	n	%
6/30/95	46	43	93.5	41	89.1	4	8.7	2	4.4	0	0.0
7/22/95	38	35	92.1	34	89.5	2	5.3	1	2.6	1	2.7
9/15/95	15	14	93.3	14	93.3	1	6.7	0	0.0	0	0.0
Average			93.0		89.9		7.1		2.3		0.9

Table 4. Number of daughter mites produced per *Varroa jacobsoni* mother mites in drone brood under Michigan conditions.

Date	All mother mites (including those producing only males and dead mites, excluding those producing only immatures)				Mother mites that produce female offspring (excluding those producing only males, dead mites and immatures)			
	Single infested cells		Total mite population		Single infested cells		Total mite population	
	n	offspring	n	offspring	n	offspring	n	offspring
6/30/95	41	2.39	48	2.29	35	2.80	41	2.66
7/22/95	76	2.45	117	1.66	27	2.81	109	1.74
9/15/95	14	2.57	44	1.66	13	2.77	42	1.70
Average		2.47		1.87		2.79		2.03

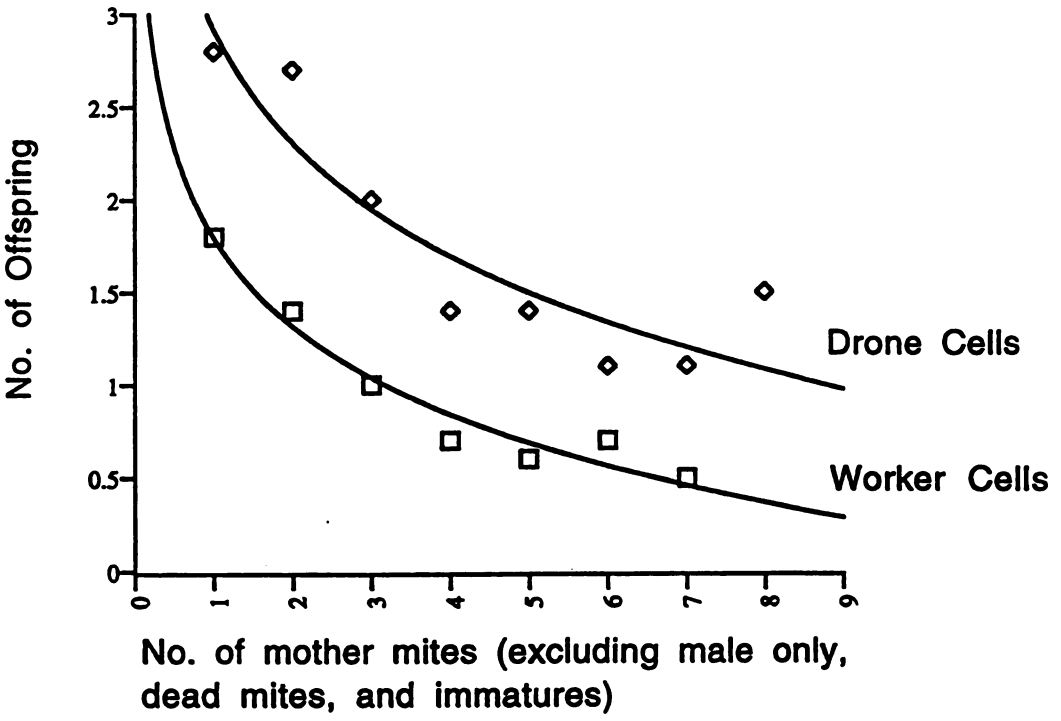

Figure 1. Average number of adult females produced by mother mites.

mothers and average offspring per mother. On average, worker cells with one mother mite produce 1.41 offspring and cells with four mothers produce 0.62 offspring in worker cells, when including male only and dead mothers (Table 5). If excluding these mother mites, the fecundity rate in worker cells would be higher: 1.82 for one mite infestations, 1.4 for two mites, 1.1 for three mites, and 0.68 for four mites. In drone cells, the increased fecundity rates are: 2.8 for one mite infestations, 2.63 for two mites, 2.23 for three mites, and 1.7 for four mites.

DISCUSSION

There is a wide variation in both fertility and fecundity rates recorded in the literature. This is at least partly due to the methodology used in the study (especially in fertility rates) and the definition of fecundity. For example, Fries et al. (1994) demonstrated that the variation in results from numerous studies was because of the different methods of reporting the data.

Comparing reproduction rates obtained in this study (Tables 1 and 3) with other studies, it is found that the mite reproduction rate of 86.8% in worker and 93% for drone broods was very representative of what other researchers found. Blum (1989) reported mite reproduction rates at 88.7%, Fuchs and Langenbauch (1989) recorded 92.7% and Buchler (1990) found 86.6% in worker brood cells. In drone cells, Fuchs and Langenbach (1989) also recorded 92.2% fertility rates in drone cells.

The percent of mites that did not reproduce (11.0% in workers and 7.1% in drones) also was similar to figures presented by other researchers. In worker cells, Sulimanovic *et al.* (1982), Schulz (1984), Moosbeckhofer *et al.* (1988), Fuchs and Langenbach (1989), Ifantidis

Table 5. Average number of offspring per mother mite taking number of mother mites per cell into consideration.

Type of cell	Mites per cell				Author
	1	2	3	4	
Workers	1.50	1.40	1.20	0.96	Moosbeckhofer et al., 1988
	1.50	1.58	1.13	0.83	Blum, 1989
	1.40	1.09	1.16	0.91	Fuchs and Langenbach, 1989
	1.60	1.50	1.70		Martin, 1994
	1.41	**1.30**	**1.00**	**0.62**	**This study**
Drones	2.21	1.90	1.52	1.51	Fuchs and Langenbach, 1989
	2.10	1.90	1.60	1.40	Martin, 1995
	2.47	**2.30**	**1.99**	**1.67**	**This study**
A. cerana drones	2.30	1.70	1.20		Rath, 1991

(1990) and Boot et al. (1995) reported infertility rates in worker cells of 13, 16, 7, 7, 14.1, and 8-12%, respectively. Fuchs and Langenbach (1989), Ifantidis (1984), and Schulz (1984) found lower levels of infertility in drone cells also. They reported 8, 4, and 5%, respectively.

Some of the mother mites produced only male offspring. This is probably because they had not mated, since haploid eggs of Varroa mites develop into males (de Ruijter and Pappas, 1983). Martin (1995) attributes this partly to the death of the male before he is able to fertilize his sisters. He found in earlier studies, that 20% of the males died before they mated in worker brood (1994) and 10% in drone cells (1995).

In this study, it was found that 5.1% of the offspring were male only in worker cells (Table 1). This was similar to other studies. Boot et al. (1995), Schultz (1994), Moosbeckhofer et al. (1988) and Fuchs and Langebach (1989) reported a rate of 8-10, 6, 3 and 3%, respectively. For drone cells, a rate of 3% was observed (Table 3). Fuchs and Langebach (1989) reported a rate of 1%.

The other parameter that was measured was the percent of mother mites that died in brood cells. It was that 2.3% died in worker cells (Table 1) and 2.7% in drone cells (Table 3). Only one other researcher reported this statistic, Martin (1994). He found a higher percentage in drones (7.7%), and a similar rate in workers (2%). He found that 32% of the deaths in drone cells were caused by failure of the mite to emerge from the brood food and found they were trapped in the cell wall. The percentage rose to 50% in worker cells.

Fecundity was measured in a variety of ways in the literature both because of different experimental techniques used and because of differing definitions of fecundity. For example, there were differences in the way that researchers extrapolated estimates where cells had to be opened before development was completed (Boots et al., 1995). In addition, some studies

included all mothers that infested brood cells, which included those that died, did not reproduce, and reproduced males only. These methods, in general, had less offspring per mother than those that excluded these groups from the study. This study compiled fecundity rates utilizing both methods in single infested cells and multiple infested cells calculated separately (Tables 2 and 4). Varroa females are biologically capable of laying up to six eggs in worker cells and seven in drone cells (Ifantidis, 1984; Martin, 1994, 1995). The fact that fecundity rates are much lower than this is attributed to offspring mortality, which occurs primarily in the deutonymph stage (Martin, 1994, 1995).

When excluding problematic mothers from the analysis, it was found that mites averaged 1.82 offspring in single cell infestations of worker brood (Table 2). In drone cells, this figure increased to 2.79 offspring (Table 4). This is fairly consistent with other researchers. Fuchs and Schulz (1984), Ifantidis (1984), Fuchs and Langebach (1989), and Martin (1994, 1995) reported 1.82 and 2.69, 1.33 and 2.77, 1.69 and 2.76, and 1.45 and 2.2 in worker and drone cells, respectively.

When including all the female mites found in single infested cells these figures decreased. In Michigan, average offspring for worker brood decreased to 1.41 (Table 2) and to 2.47 for drones (Table 4). These statistics differed widely among other researchers. Schulz (1984) found 1.3 in worker cells and 2.6 in drones. Ifantidis (1984) reported 0.71 in worker and 1.7 in drone cells. Fuchs and Langebach (1989) found 1.4 in worker and 2.21 in drone.

When the whole mother mite population is taken into consideration (single and multiple infested cells), the average number of offspring decreases for both calculation methods (Tables 2 and 4). The negative correlation of average offspring per mite and

number of mother mites infesting the cell is well documented in the literature and is supported by the study reported here (Figure 1, Table 5). The Michigan data includes both dead mothers and only male reproduction.

Fuchs and Langenbach (1989) attribute this lower fecundity rate to suppressed reproduction while Martin (1995) shows that it is due largely to increased mortality of the offspring. Donze and Guerin (1994) showed that mites normally feed at a single feeding site. Martin (1995) explained that with increased number of eggs, there is more competition for the feeding site, and stronger deutonymphs and adults will out compete younger offspring.

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MODELING OF HONEY BEE AND MITE POPULATION DYNAMICS

ABSTRACT

The life history of the honey bee *Apis mellifera* and the bee mite *Varroa jacobsoni* and their interactions were modeled using a commercial software package known as Stella II. Stella II provides a non-mathematically intensive modeling technique that allows the user to generate a series of differential equations that can track a population through time with a minimum set of parameters. The model generates population statistics at regular intervals throughout a designated time period and outputs diagrams, a series of equations, tables and graphs.

Mite parameters included in the model are: initial mite population, number of female offspring per mother mite in both worker and drone brood, number of reproductive cycles, fertility, mite preference for drone versus worker brood, phoretic period, mortality, and removal of infested brood cells.

Interaction between the bee and mite population were also modeled. For example, the impact of various mite infestation levels on honey bee colony dynamics was modeled using three different mite initial infestations rates (5, 10 and 20 mites). The first year infestation rate resulted in different maximum mite populations levels, and the actual estimate was 690, 1,339 and 2,521 for the three rates, respectively. In the second year, the mite population

maximums grew to 11,000, 17,000 and 25,000, respectively. However, the colony collapse was inversely proportional to the initial infestation rate. For example, the colony with an initial rate of 20 mites collapsed first.

It is also possible to change other parameters of the model such as post-capping period, fertility and fecundity rate, or to introduce chemical and biological control mechanisms. These simulations may help beekeepers alter their control strategies for the mites.

The objective of this modeling project is to develop a tool that will both predict bee and mite populations under specific conditions and allow a scientist to vary and check the influence of single factors on the mite population development. In addition, it will help in the development of research hypotheses to test under field conditions. It also was the hope of this modeling project to integrate past research results and identify research gaps that need further investigation in an effort to find better ways to control mite populations in bee colonies.

INTRODUCTION

Modeling is a valuable tool that helps in the understanding of the complex societies, such as honey bees, by incorporating the many factors that compose or influence the colony population dynamics.

There have been several models developed that describe honey bee colony population dynamics. Degrandi-Hoffman *et al.* (1989) developed a model that simulates honey bee (*Apis mellifera* L.) colony population dynamics. Her model was based on the egg laying potential of the queen, foraging characteristics of the colony, degree days, and amount of

sunlight. Harris (1985) developed a model that predicts adult honey bee population dynamics based upon field estimates of sealed brood or daily egg laying rates, survival rates of the immature and adult bees, developmental rates of eggs, larvae, and pupae, and the initial size of the adult population. McLellan *et al.* (1980) and Rowland and Mclellan (1982) developed models to predict brood production throughout the year based upon algorithms describing the increased and decreased egg laying potential.

In addition, there have been models developed for the Varroa mite. Camazine (1988) modeled some factors affecting severity of Varroa on European and Africanized bees. Omholt and Crailsheim (1991) developed a model to predict the degree of infestation of honey bee colonies estimated by a mean of their natural death rates. Fuchs (1992) demonstrated in model simulations the importance of choice between worker and drone brood cells at varying ratios of the brood types for optimal reproductive success of the mite. Fries *et al.*, (1994) developed a comprehensive model based on both bee and mite population dynamics. However, their bee population dynamics were static and did not change with mite interactions. Marcangeli *et al.* (1995) used Camazine's model to analyze the population growth of *V. jacobsoni* in the temperate climate in Argentina.

The population dynamics of a honey bee colony is dependent on many parameters that interact with each other. These include oviposition, colony population, weather and brood availability. The egg laying has the most dramatic effect on colony population dynamics (DeGrandi-Hoffman *et al.*, 1989; McLellan *et al.*, 1980).

Egg laying potential depends on sunlight, degree days, and the foraging population. Under Midwestern conditions temperature ranges for egg laying is between 0-31C°, and the

photoperiod between 9.1 to 15.25 h. of light per day (DeGrandi-Hoffman *et al.*, 1989). Nolan (1925, 1928) found that egg-laying rates of less than 2,000 per day over a 12-day period were to be expected.

According to Fukuda & Sakagami's (1968) life table, 95.8% of the eggs hatch and become unsealed brood. After five days, 85.7% of the unsealed brood become sealed brood. Twelve days later, 98.8% of the sealed brood emerged as adults. During their twenty one days as house bees in the hive, 5.54% die.

It takes approximately 21 days for eggs to become adult workers and 24 days for eggs to become adult drones (Jay, 1963). It is estimated that the egg and larvae mortality rate is approximately 19% (Fukuda & Sakagmi, 1968). The natural adult bee life span depends on the season (Ribbands, 1953; Fukuda & Sakagami, 1968). The average longevity of June bees is 28.3 days, July bees 32.4 days, wintering bees 154.1 days and postwintering 23.4 (Fukuda and Sakagami, 1968). Under optimal colony conditions, the adult drone life span was estimated to be 59 days (Howell and Usinger, 1933). It is normal to expect a 50% decline in honey bee population during the winter (Avitabile, 1978).

Under Midwest conditions, colony populations peak at most at 50,000 adults in the middle of July while drone populations tend to peak in the middle of June. Bees do not produce brood from late autumn to midwinter (late January) and are confined to the hive (I. e., do not forage) from late October to early April (DeGrandi-Hoffman *et al.*, 1989).

All factors that increase the brood activities of the bees have a strong effect in the development of the mite populations because the growth of the mites population is closely correlated with the availability and type of brood.

In addition, mite population is effected by factors such as fertility and fecundity of the mite, reproductive cycle, phoretic period and mortality either natural or caused by the bees as result of hygienic or grooming behavior of the bees.

Koeniger *et al.,* (1981) and Anderson (1994) reported that *V. jacobsoni* does not normally reproduce when it infests worker brood of the Eastern honey bee, *A. cerana.* Extensive mite reproduction occurs only on drone brood. In *Apis mellifera*, a portion of the infesting Varroa mites do not reproduce. Blum (1989) reported mite reproduction rates at 88.7%, Fuchs and Langenbauch (1989) recorded 92.7% and Buchler (1990) found 86.6% in worker brood cells. In worker cells, Sulimanovic *et al.* (1982), Schulz (1984), Moosbeckhofer *et al.* (1988), Ifantidis (1990) and Boot *et al.* (1995) reported infertility rates in worker cells of 13, 16, 7, 4.1, and 8-12%, respectively. Fuchs and Langenbach (1989) , Ifantidis (1984), and Schulz also (1984) found lower levels of infertility in drone cells. They reported 8, 4, and 5%, respectively. Ritter and De Jong (1984) observed only 43% of the mites in *A. m. ligustica* in the worker cells in South America to be fertile. Marcangeli *et al.,* (1992) estimated that, depending on the season, between 56% and 72% of the mites in *A. m. ligustica* colonies were fertile. Rosenkranz and Engels (1994) compared Africanized and European colonies of *A. mellifera*, and found less than 40% of female mites were fertile in Africanized bees, whereas, in European bees between 80-90% were fertile.

Ruttner (1984) reported colonies in Uruguay which could resist Varroa infestation without any treatment; this was attributed to the very low fertility (10-30%) of the mite in worker brood cells. In Tunisia, Ritter (1990) reported the comparatively low number of fertile mites produced (50-80%). This demonstrated the increased tolerance of *A.m. intermissa* to Varroa.

The number of offspring produced by Varroa females is also an important factor effecting the mite population. The number of offspring depends on the type of brood, that they are produced on, whether it is worker or drone cells. Schulz (1984) measured offspring reproduction by fertile female mite in worker brood as 1.8 (including infertile mites 1.6). For the drone the reproductive factor was 2.7. Fuchs and Schultz (1984), Ifantidis (1984), Fuchs and Langebach (1989), and Martin (1994, 1995) reported 1.82 and 2.69, 1.33 and 2.77, 1.69 and 2.76, and 1.45 and 2.2 in worker and drone cells, respectively.

The number of times a mother mite enters a brood cell to reproduce is a key factor in determining the population growth of *V. jacobsoni* (Fries *et al.*, 1994). Ruijter (1987) artificially transferred mites from cell to cell and found that the mother mite is able to reproduce as many as seven times. Schulz (1984) reported that 78% of the mites reproduce only once and 22% reproduce twice. Mikityuk *et al.* (1976) observed an additional reproduction cycle. He stated that 78% of the Varroa produce only once, 18% produce twice and 4% produce three times for an overall mean number of 1.26 reproductive cycles per female mite. Mikityuk (1979) stated that 1.9% of the mites reproduce four times. Fries and Rosenkranz (1993) reported that 13% of the mites reproduce three times, their sample size was 475 mother mites. Wended and Rosenkranz (1993) found that 4.1% of the mites produce three times with an overall mean of 0.88 reproductive cycles per mother mite. Recently, Fries and Rosenkranz (1996) using full-size colonies reported that under optimal conditions the mean number of reproductive cycles by Varroa is greater than 1.5 but less than 2.

After emergence from the brood cells, the female mites reside a certain period on adult bees in the colony before they invade new brood cells (Boot *et al.*, 1993; Boot *et al.*, 1994). Boot *et al.*, (1995) stated that the length of this period strongly affects the population

dynamics of the mite, because mites cannot reproduce while they reside on adult bees and therefore reproduction is delayed. In addition, the period on adult bees may affect the population dynamics of the mites since some of the mites will die during their stay on adult bees and it might reduce the number of offspring per mother mites (Beetsma and Zonneveld, 1992). Thus, mite fitness increases by minimizing their stay on adult bees (Boot *et al.* 1993). Schulz (1984) reported after a phase of 1-20 days (44% within 6 days) on adult honey bees, the female mite enters the brood cell for reproduction. He found that the phoretic period was 4.5 days for older mites, 10.7 days for younger mites and averaged 7.4 days for a mixed population of mites. Boot *et al.* (1993, 1994) stated that during the brood rearing the mean residence time of mites on adult bees is maximally 1-3 weeks, depending on the number of brood cells available for mite invasion. Woyke (1987) reported that mites have an average phoretic period of 4.7 days in a mixed population and 5.9 days for younger mites. Grobov (1977) reported a range of 4-13 days.

Mites begin to invade brood cells during a limited period preceding cell capping with a fairly constant rate until cells are capped, about 50 and 20 hours for drone and worker, respectively (Ifantidis 1988 and Boot *et al.* , 1992).

Muller (1987) stated that the Varroa mite does not change hosts if the host drops from the winter cluster. A 50% reduction in the number of bees is normal during wintering in cold climates (Avitabile, 1978), and a similar effect on the population of Varroa could be expected (Fries *et al.*, 1991). Muller (1987) reported losses of between 3 and 38 mites per day throughout the European winter. However, other authors suggested different percentages, 3-10% (Weiss, 1984; Rademacher and Geiseler, 1986); Moosbeckhofer (1991) reported

between 3% and 40%; Korpela *et al.* (1992) estimated a total mortality of 40% over a broodless period of 125 days during the winter, which corresponds to a mean mortality of 0.4% per day. Boot *et al.* (1995) estimated 0.6% per day during the brood rearing periods and stated that there is no reason to think that mortality of mites on adult bees should depend much on the time of the year.

Fries *et al.* (1994) stated that one important source of summer mortality of phoretic mites is the loss of mites on foragers that fail to return to the hives. A colony whose population is in steady state will have approximately 1,500 adult bees eclosing and dying each day, or about 5% of the population. Mite mortality in the sealed brood cell is approximately 1.5% of the mother mites (Kustermann, 1990).

Hygienic and grooming behavior also has an effect on mite populations. In the Asiatic honeybees *A. cerana* F., the original host of *V. jacobsoni,* the infestation remains at low levels and the parasite does not severely harm the colony. That may be due to the number of defense mechanisms that this bee has. One of these mechanisms, as described by Peng *et al.* (1987), is the active removal of adult mites from the bodies of worker bees. This process involves self-cleaning behavior. After showing signs of irritation, the bee performs a grooming dance, and then nestmate cleaning and group cleaning behavior. This resulted in removing (within two hours) more than 99% of mites added to the colony. Only 0.3% of the mites were removed by grooming in colonies of *A. mellifera.* Buchler *et al.* (1992) also compared grooming in *A. cerana and A. mellifera* and found successful mite were removal in 75% of the cases in *A. cerana.* In *A. mellifera,* 48% of the mites removed by grooming. Fries *et al.* (1996) reported lower numbers in full-sized colonies of *A. cerana,* 56% of 220

mites were removed by the bees in 6h. and, of those, 30% were damaged; results for *A. mellifera* colonies were 21% of 280 mites were removed and 12% were damaged.

Ruttner and Hanel (1992) examined the natural mortality of five *A. m. carnica* colonies for about one year and found on average 26% of the mites collected from inserts showed injuries to the legs but rarely to the cuticle of the idiosoma. Moretto *et al.* (1991) reported that 5.75% of the mites were removed by *A. m. ligustica* bees within 30 min after infestation, and an average of 38.5 (range 10-70%) were removed by Africanized hybrids of *A. mellifera* bees.

Hygienic behavior of bees was described by Rothenbuhler (1964) in relation to resistance against American foulbrood (*Bacillus larvae*). He showed that hygienic behavior consists of two independent behavioral events: the uncapping of cells containing larvae or pupae, and the removal of the dead brood. The hygienic behavior of *A. mellifera* against Varroa mites was observed in both *A. cerana* and *A. mellifera*. Rath and Drescher (1990) showed that the *A. Cerana* workers were success at detecting, uncapping and removing 98% of artificially infested worker brood cells within 5 days. Boecking and Drescher (1990) reported that artificially infested worker brood cells were detected, uncapped and removed to various degrees and they show that brood cells infested with one Varroa mite were rejected from 14.3 up to 95.8%, those with two Varroa from 25 up to 100% after ten days. Boecking and Drescher (1991) reported that the removal of brood cells infested with one mite in *A.m. carnica* was 5.5% (minimum) up to 95.8 (maximum). Within the same colonies; brood cells infested with 2 Varroa mites showed a removal from 4.8% (minimum) to 100.0% (maximum). In another study Boecking and Drescher (1994) stated that mites more

effectively removed infested brood from their cells. When one mite was in a cell, the removal rate are 10.9% for their own brood and 15.4 for another brood, when number of mites increased to two, removal rates rose to 32.2% and 41.9%, respectively.. Boecking and Ritter (1993) reported workers in 15 test *A. m. intermissa* colonies detected and removed up to 75% of artificially infested brood and removed up to 97-99% of freeze-killed brood in each of two trials.

MATERIALS AND METHODS

The bee and mite population dynamics were modeled using a modeling package known as Stella II (High Performance Systems). Stella provides a non-mathematically intensive modeling tool that automatically computes mathematical equations. The program presents the model in a variety of ways, such as through diagrams, a series of equations, tables and graphs that represent model inputs and outputs that are simulated through a specific time. The model was constructed using literature values (Table 1) to simulate honey bees, *Apis mellifera* and *Varroa jacobsoni* population dynamics.

Model description

This biological model has two major components, one focusing on the honey bee and the other on the mite (Figures 1 and 2). It simulates five years of colony development with 1800 time intervals (one per day). The initial model assumes that the bee population begins with 15,000 adults and the mite is introduced with an initial population of 10 mites. The model is designed so the user can change these initial parameters.

Bee submodel. The honey bee component of the model is largely driven by the number of eggs laid per day (Figure 3). The eggs laid per day equation is first based on the

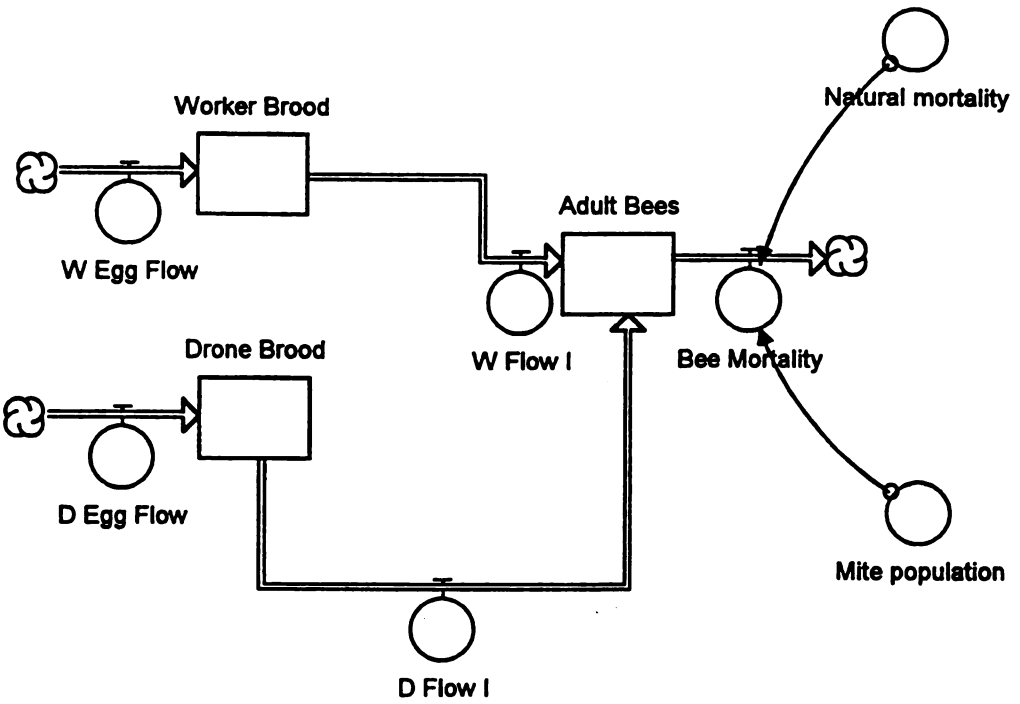

Figure 1. Honey bee component of the modelling project.

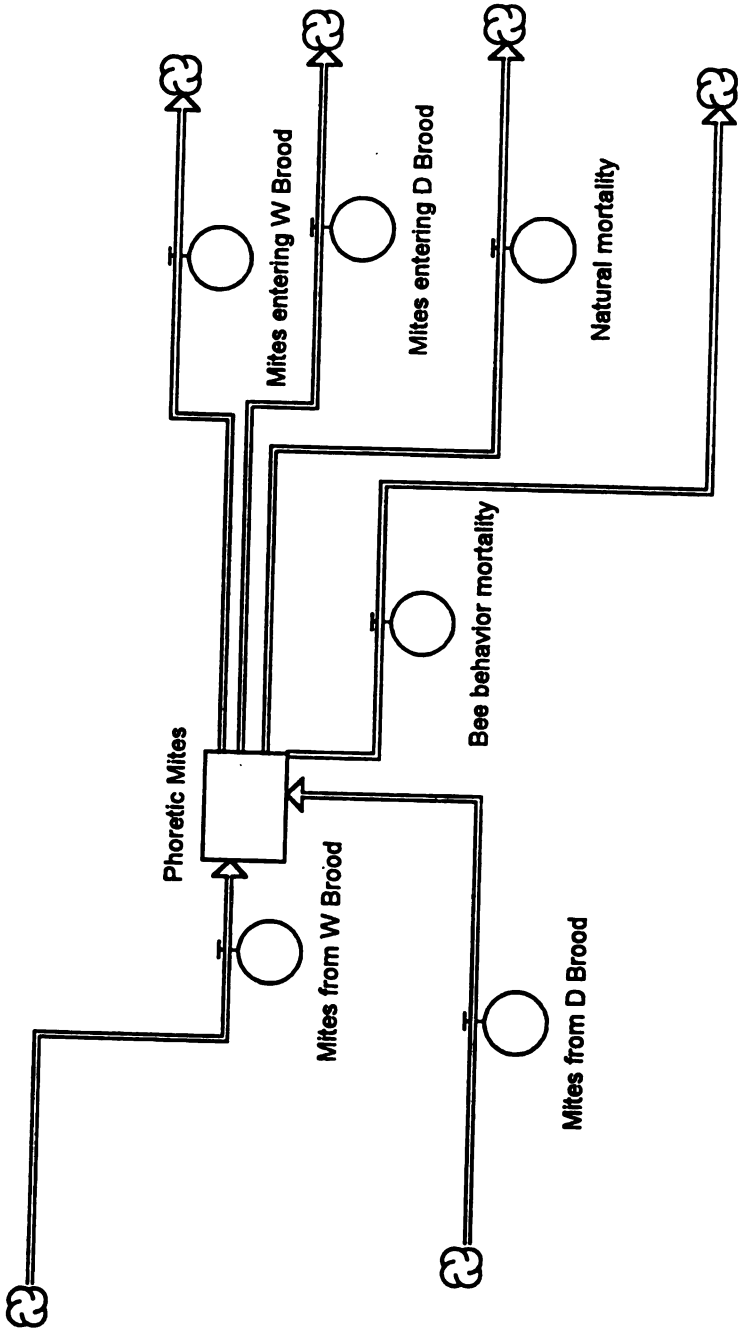

Figure 2. Mite component of the modelling project

Table 1. Parameters used for model simulation of *Varroa jacobsoni* and honey bees *Apis mellifera*.

Systems Parameters	Honey Bee	Mite
Initial Population	10,000	10
Length of simulation	5 years	5 years
Length of time interval	1 day	1 day
Starting date	January 1	January 1
Maximum eggs laid per day	1500	***
Brood Mortality	0.15 (Sakagami and Fukuda, 1968)	***
Hours of sunlight	Michigan average accumulated sunlight)	***
DD	50 year average of acc. temperature with base of 0°C (Published database on max/min temperatures on CD Rom)	***
Foraging	Percent foragers under Midwestern conditions (DeGrandi-Hoffman, 1989)	***
Adult factor	Coefficient of adult factor taken from Midwes research data (DeGrandi-Hoffman, 1989)	***
Worker postcapping period	12 days	***
Drone postcapping period	14 days	***
Total worker brood	Conveyer stock, with 12 day interval	***
Total drone brood	Conveyer stock, with 14 day interval	***
Worker proportion	Graph function, Table 1 (Nolan, 1925,1928)	***
Natural mortality	Graph function (Sakagami and Fukuda ,1968)	Graph function (.004 for winter, .006 for summer) (Fries *et al.*, 1994; Boot *et al.*, 1996)
Bee Mortality due to mite invasion	Dependent on no. of mites per pupa (Beetsma, 1983)	
Mite Mortality due to bee mortality		Mites on infested bees will die with bee, additional mortality is equal to the number of mites on bees that die (Muller, 1987), see equation 8.
Phoretic Period	***	5.9 days (Woyke, 1987)
Mite preference for drones (fraction to drones)	***	Graph function (Fuchs, 1990)
Number of offspring per mite		Graph function, Table 4
Mite fertility on worker brood	***	0.85 (Schulz, 1984)
Mite fertility on drone brood	***	0.95 (Schulz, 1984)
Number of reproductive cycle	***	1.4
Number of female offspring produced in a worker cell Number of female offspring produced in a drone cell		1.3 (Ifantidis, 1984) 2.7 (Schulz, 1984; Ifantidis, 1984)

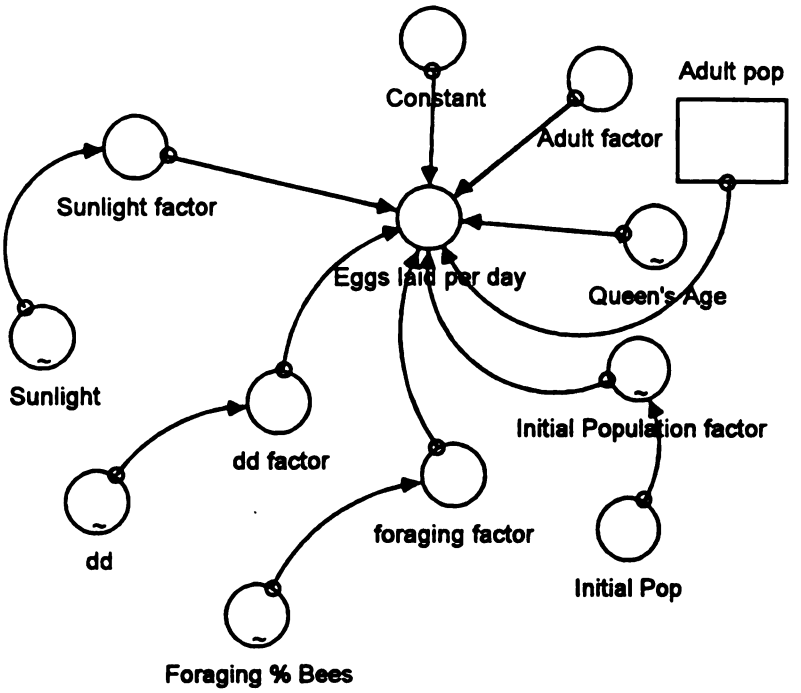

Figure 3. Honey bee egg laying components of the modelling project.

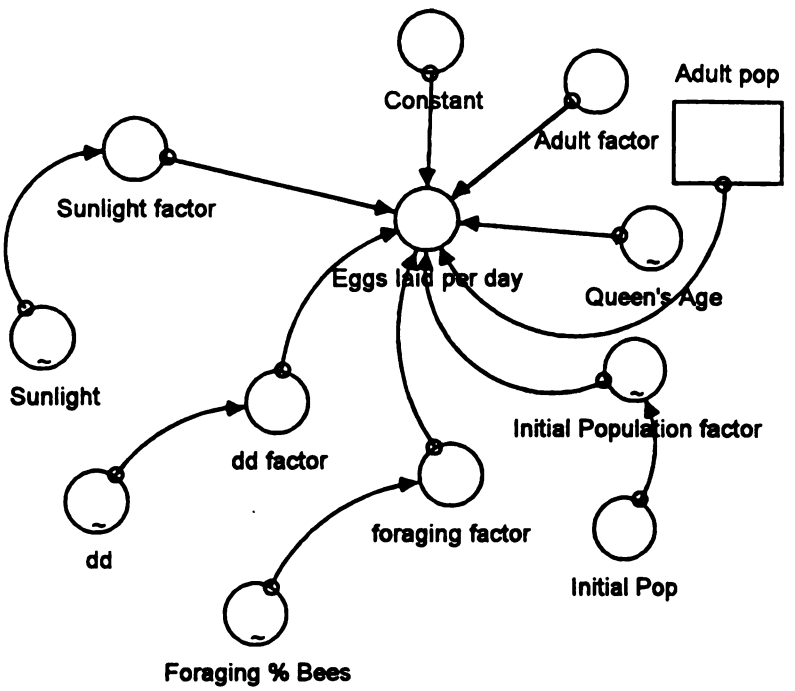

Figure 3. Honey bee egg laying components of the modelling project.

assumption that the adult population must have at least 1,000 members to support the queen's egg laying (If Adult population > 1000 then use the regression line to estimate number of eggs laid, otherwise enter 0). If the population is greater than 1,000 the regression equation is the primary factor determining egg laying potential unless it returns a negative value. If it returns a negative value then, once again 0 is entered as the number of eggs laid that day. The regression equation was based on four factors and a constant. These factors included: sunlight, degree days, foraging and number of adults in the colony. These factors explained 95.5% of the variability in egg laying ($p<0.001$).

$$E = -1303 - 0.0154A + 188.703S + 0.859D + 5.525F \qquad \text{Eq. 1}$$

where:

E = Maximum number of eggs laid per day
A = Number of adults in bee colony
S = Hours of sunlight
D = DD accumulation incremented per day
F = Percent of foragers in bee colony

If the regression equation is positive, that number of eggs is multiplied by two factors, one corresponding to the age of queen and the other to the size of the initial adult population. The queen's age coefficient ranges from 0.9 to 1.0, depending on the age of the queen. Older queens do not lay as many eggs. In addition to queen's age, it is believed that number of worker bees have a positive correlation to egg laying. If the initial population is low, the number of eggs laid does not meet the queen's egg laying potential. However, if the population is 15,000 or more, then the queen lays eggs close to her potential. The initial population factor ranged from 0.75 to 1.25, depending on the size of the colony (ranging from 1000 to 30,000).

Eggs develope to worker or drone brood. The proportion that became worker brood was multiplied by the number of available eggs. The rest (one minus the proportion becoming worker brood * available eggs) develop to drone brood. The proportion that develops to worker and drone brood was dependent on time of year and taken from Michigan specific research papers.

A delay function was used to determine the number of eggs going from the egg stage to the brood stage for both drone and workers. This function allowed a three- day delay, which is the biological development time for the egg. More specifically, if the queen laid the egg on day 1, it would pass through the egg phase on day 4. The number of eggs available at any given time was accumulated in separate stocks for worker and drone eggs. The equations are as follows:

$$dE_D(t) = E_D(t\text{-}dt) + (E_D(t)\text{-}F_{DI}(t))dt \qquad \text{Eq. 2a}$$

$$dE_W(t) = E_W(t\text{-}dt) + (E_W(t) - F_{WI}(t))dt \qquad \text{Eq. 2b}$$

where:

dE_D = Change in drone eggs
F_{DI} = Flow from drone eggs
dE_W = Change in worker eggs
F_{WI} = Flow from worker eggs

This number was then multiplied by an egg mortality factor before it entered the brood stock, which once again was accumulated. The mortality rate was 0.15 for workers and 0.35 for drones. The brood accumulated as follows:

$$dB_D(t) = B_D(t\text{-}dt) + (0.65*F_{DI}(t) - F_{DII}(t))dt \qquad \text{Eq. 3a}$$

$$dB_W(t) = B_W(t\text{-}dt) + (0.85*F_{WI}(t) - F_{WII}(t))dt \qquad \text{Eq. 3b}$$

where:

dB_D = Change in drone brood
B_D = Drone brood
F_{DI} = Eggs becoming drone brood
F_{DII} = Flow from drone brood
dB_W = Change in worker brood
B_W = Worker brood
F_{WI} = Eggs becoming worker brood
F_{WII} = Flow from worker brood

The developmental period for larvae was 21 days for drones and 18 days for workers. Therefore, the total number of drone brood is equal to the number of brood already present, plus the number entering that specific day from the eggs laid three days previously, minus the number of brood becoming adult bees, either those entering the brood 21 days before (drones) or 18 days for the workers.

Total honey bee population was determined by the number of honey bees already present, plus the honey bees coming from brood cells, minus honey bees lost due to mortality factors. The mathematical equation for bee population growth is:

$$dBP(t) = BP(t-dt) + (F_{WII} + F_{DII} - M_{BP})dt \qquad \text{Eq. 4}$$

where:

BP = Bee Population
F_{WII} = Flow from worker brood
F_{DII} = Flow from drone brood
M_{BP} = Bee Population Mortality

Honey bee mortality came from either death due to natural causes or death due to varroaosis. Honey bees typically survive 32 days in the summer, and 154 days in the winter. If the bee had one mite enter its pupa cell, the bee's life span is reduced by one-third; and if two or more mites entered its brood stage, its life span is reduced further (by about two-

thirds). These mortality rates were also taken from the literature. Thus, the equation for bee mortality is as follows:

$$M_{BP} = (BP - MP_{DC} - MP_{WC})*MB + (MP_{DC} + MP_{WC})*2*MB \qquad \text{Eq. 5}$$

where:

M_{BP} = Mortality of bee population
BP = Bee Population
MP_{DC} = Mite population entering drone cells
MP_{WC} = Mite population entering worker cells
MB = Mortality rate for bee

Mite submodel. Once a bee colony was established, the model assumed that mites were introduced into the system. In many ways, the mite population dynamics is much more complicated than the honey bee. It depends on both the bee population and the density of the mites in relation to the bee population (Figure 4).

The mite population dynamics begins with the number of phoretic mites and their density compared to the number of available worker and drone brood cells. The number of phoretic mites is a function of the number of mites already present, plus the mothers and offspring exiting worker and drone brood, minus mite mortality, minus mites entering into worker and drone brood that are available for reproduction. The number of phoretic mites in a colony at any given time is represented by the following equation:

$$dMP(t) = MP(t-dt) + (MP_{ED} + MP_{EW} - M_{MP} - MP_{DC} - MP_{WC})dt \qquad \text{Eq. 6}$$

where:

dMP = Change in mite population
MP = Mite population
MP_{ED} = Mite population exiting drone cells
MP_{EW} = Mite population exiting worker cells
M_{MP} = Mortality of phoretic mites
MP_{DC} = Mite population entering drone cells
MP_{WC} = Mite population entering worker cells

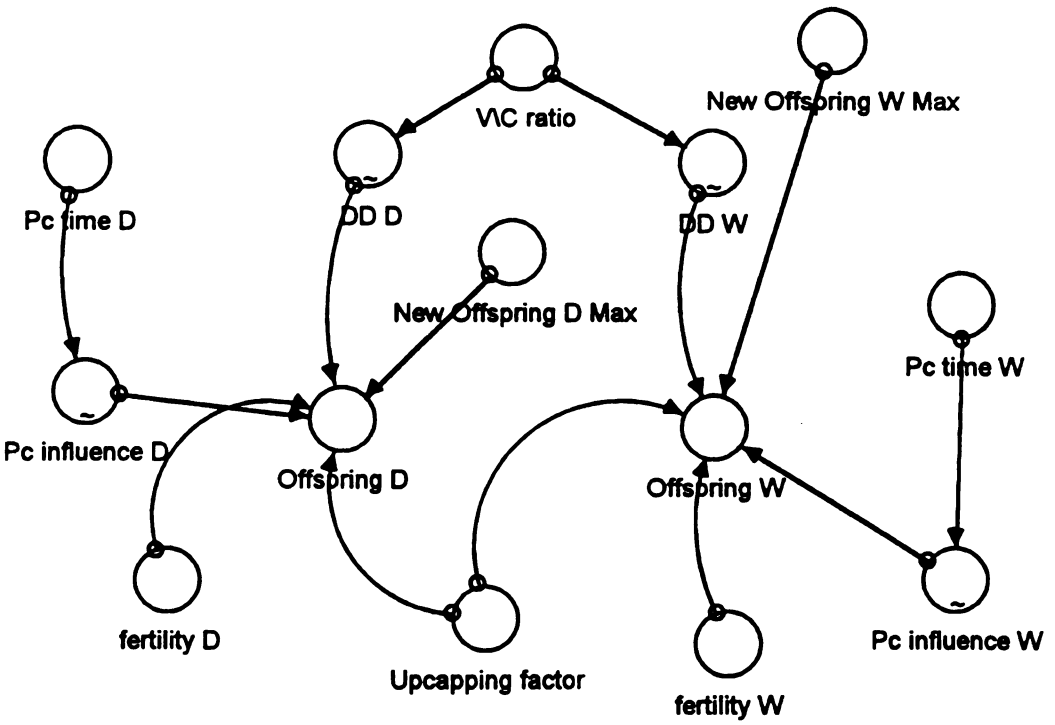

Figure 4. Mite population components of the modelling project.

When mites are ready to reproduce offspring, they enter brood cells, with a preference for drone brood cells. The number that enter each brood cell is very important because it determines the number of offspring that each female will produce. The actual number of offspring is determined by the fertility rate of the mite, the number of female mites available to produce eggs, the number of available worker and drone brood cells, and the length of the post-capping period.

The mites have a higher fertility rate in drone cells (0.95) than in worker cells (0.85) and can also produce more offspring in drone cells (up to 2.7) than in worker cells (up to 1.3).

The equations for offspring produced in worker and drone brood is as follows:

$$O_{WB} = F_W * DD_W * I_W * UF \qquad \text{Eq. 7a}$$

$$O_{DB} = F_D * DD_D * I_D * UF \qquad \text{Eq. 7b}$$

where:

O_{WB} = Offspring produced in worker brood
F_W = Fertility rate in worker cells
DD_W = Density dependence in worker cells
I_W = Post-capping influence in worker brood
UF = Uncapping factor
O_{DB} = Offspring produced in drone brood
F_D = Fertility rate in drone cells
DD_D = Density dependence in drone cells
I_D = Post-capping influence in drone brood

Density dependence for mite offspring in worker and drone brood depends on the number of mites entering each cell. This is dependent on both the number of mites and the number of cells available. The number of available cells is determined by the total number of cells that are of the correct age to attract the mite. This part of age corresponds to the eighth and ninth day after egg laying plus an additional two hours on the tenth day for drone

brood, and to 20 hours of the eighth day for worker brood. Delay functions were used to simulate this period of attraction. Total number of available drone brood cells was equal to the number of eggs laid eight days previously plus the number of eggs laid nine days previously plus one-twelfth times the number of eggs laid ten days ago, while, total number of available worker brood cells was equal to the number of eggs laid eight day ago, multiplied by 20/24 as the attractive period is equal to 20 hours.

Then the number of mites available to enter the cells was divided by the number of brood cells available to determine the average number of mites per cell. This amount determined the number of offspring each mite would have. This density dependent offspring function ranged from 0.0 to 3.0 for drone brood cells, with number of offspring falling from 3.0 to 0.0 when number of mites per cell was greater than 6.0. The range was less for worker cells, extending from 0.0 to 1.3, with the number of offspring falling to 0.0 when number of mites per cell was greater than 3.0.

Post-capping period was dependent on type of brood cell. Worker brood had a period of 12 days and drone brood 14 days. It is assumed that there is a small amount of variation in the actual Post-capping time, and if the time is somewhat shorter less mite offspring will be produced. Post-capping influence is a function that ranges from 0.5 to 1.5 which reflects the influence of the variability of the Post-capping period on reproduction. The model assumes that the Post-capping period is a random function, and is normally distributed with a mean of 12 and a standard deviation of 0.1 for workers; and a mean of 14 and a standard deviation of 0.1 for drones.

Total number of mite offspring is multiplied by 0.95 due to an uncapping factor. Adult worker bees will destroy brood cells if they know that the mites are present and this accounts for a mortality rate of approximately 0.05.

The number of offspring is multiplied by 1.4 which is the average number of reproductive cycles per female mite to obtain the number of mites leaving drone and worker cells to become phoretic mites.

Therefore, the total number of mites exiting worker and drone cells is a combination of the number of mothers entering the cells and the number of live offspring that each produces.

Mite mortality is a function of natural mortality. Since the mite life expectancy is approximately twice as long as the honey bees, the honey bee mortality rate was used for the mite but it was multiplied by 0.5. An additional mortality factor is due to honey bee mortality because if a phoretic mite is on a honey bee it will die if the honey bee dies. The mite will not leave the dead bee. In addition, approximately 1.5% of the mother mites died in the sealed brood. The equation for mite mortality is as follows:

$$M_{MP} = (M_P * M_B) * .5 + 0.015 * (MP_{DC} + MP_{WC}) \qquad \text{Eq. 8}$$

where

M_{MP} = Mite population mortality
M_P = Mite population
M_B = Mortality rate for bee
MP_{DC} = Mite population entering drone cells
MP_{WC} = Mite population entering worker cells

RESULT AND DISCUSSION

The model simulates bees and mites populations and illustrates the effect of the bees on the mite population and the effect of the mites on the bee population.

The model incorporates information from previous models such as models cited in Degrandi-Hoffman *et al.* (1989) and Fries *et al.*, (1994) and from experimental data. The model has the flexibility to alter some of the parameters that effect both bees and mite populations. By altering those parameters, the model will be a valuable tool that indicates which values have the most effect on populations. This should lead to more effective application for control or more effective bee breeding programs to select for tolerant or resistance bees.

When starting with 10,000 adult bees in January, the colony population peaked at 50,000 adults in the end of July (Figure 5). Worker brood population peaked at about 19,000 in the end of June while drone brood started in the end of March and peaked at about 1,900 the first week of June (Figure 6) with a ratio of about 11/89 to workers. The egg laying was maximum the first week of June at about 1,500 eggs/day.

When starting with higher initial population in January the population will remain higher and the peak is higher. Figure 5 shows that there are almost 7,000 more adults if the model starts with 5000 more initial population. The colony will enter the winter with about 2,000 more adult bees which will result in more bees the following spring. These results are in agreement with Nolan (1925) and Degrandi-Hoffman *et al.* (1989). Under Midwest conditions, the overwinterd colony must be over 10,000 in January to be able to survive and the number of bees will strongly effect the initiation and amount of egg laying because more

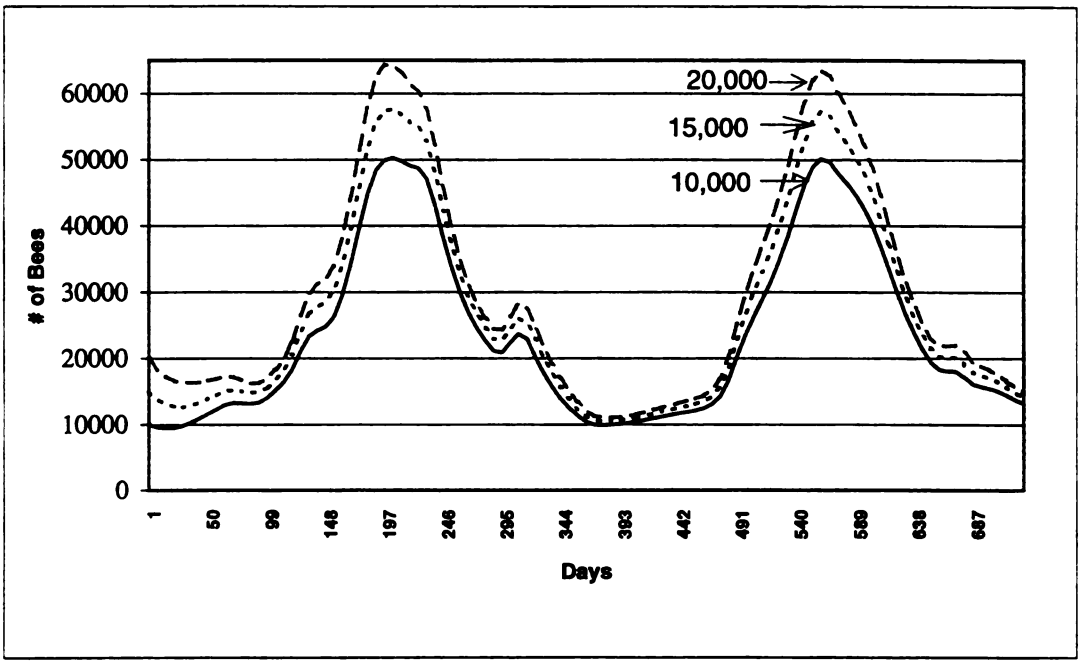

Figure 5. Adult bee population development when starting with different initial populations in January

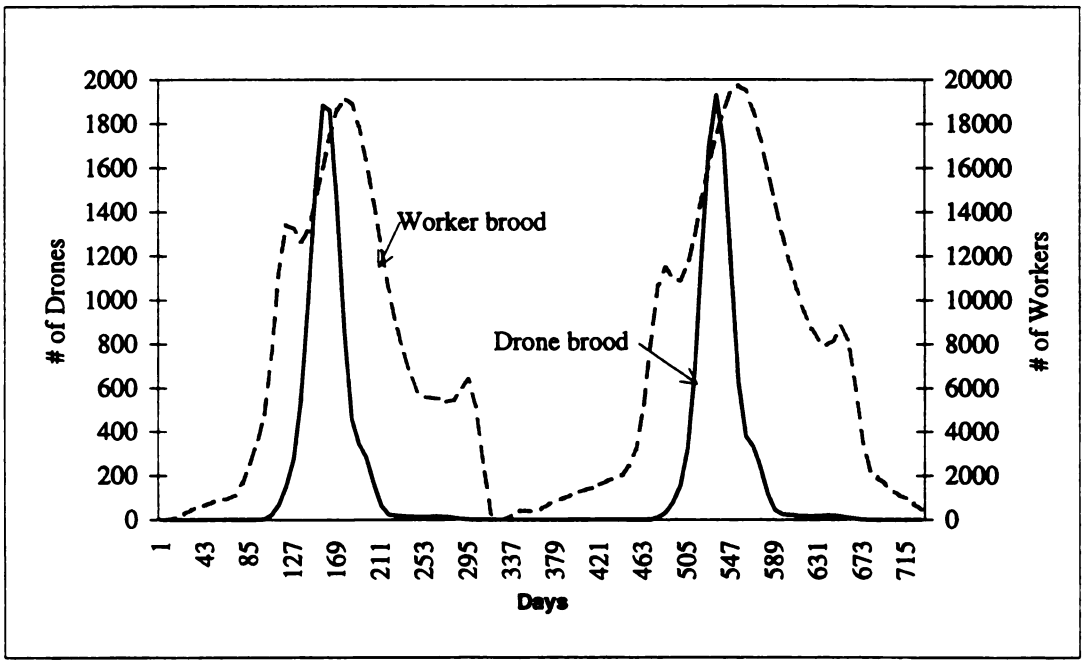

Figure 6. Worker and drone brood population development.

bees are needed to increase the nest temperature to the degree where the brood will be able to survive.

When using the values in Table 1, and starting first of April with 10 mite's, about 10,000 bees and about 4,000 worker brood cells. The infestation will stay relatively low until the drone and worker populations reach their maximum. At this time the number of mite will increase sharply (Figure 7). The relatively high amount of brood in September and early October and the increased mite population resulted in mite population peak at about 1,375 in the end of October (Figure 7). The second year, the bee population decreases up to the end of August and dies early September (Figure 9). These results concur with the study by Ritter (1984).

The times at which a certain mite number is reached, as well as whether these numbers lie above the damage threshold, depends mainly on the initial degree of infestation in Spring (Ritter, 1988), the amount of the brood reared and the degree of immigration. Figures 8 and 10 shows the mite population with different initial infestation. Starting with 5, 10 or 20 mites, result will be peak populations of 690, 1,339 and 2,521 in the first year, and as the initial infestation increases, the population peaks early in the season in the second year. The same trend will continue the next year until the damage threshold is reached. It seems that the threshold depends on the ratio of mites to bees. If the number of mites is high in proportion to bees, the bee population can not support the colony and it will die.

Mite population has been studied in USA recently (Delplane and Hood, 1997) in Georgia Started with new packages of bees which contained a small incipient population of *V. Jacobsoni*. The mite population development was in June 427±110, in August 3172±324 and 6662±2127 in October. In their experiment, the development of mite population in

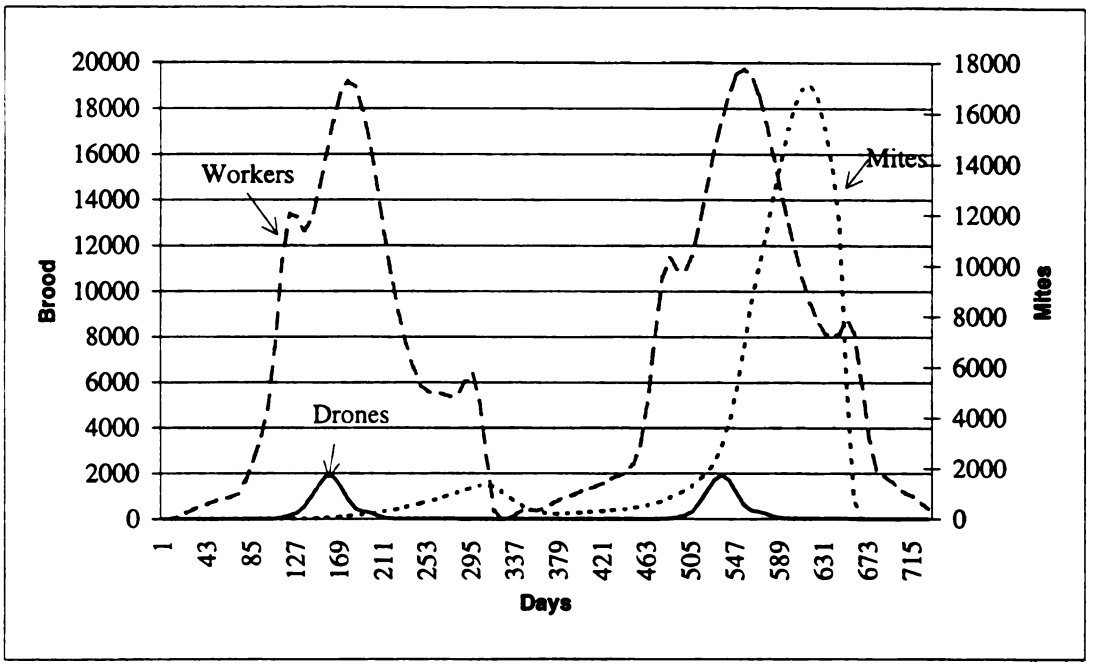

Figure 7. Mite population in correlation with worker and drone brood development.

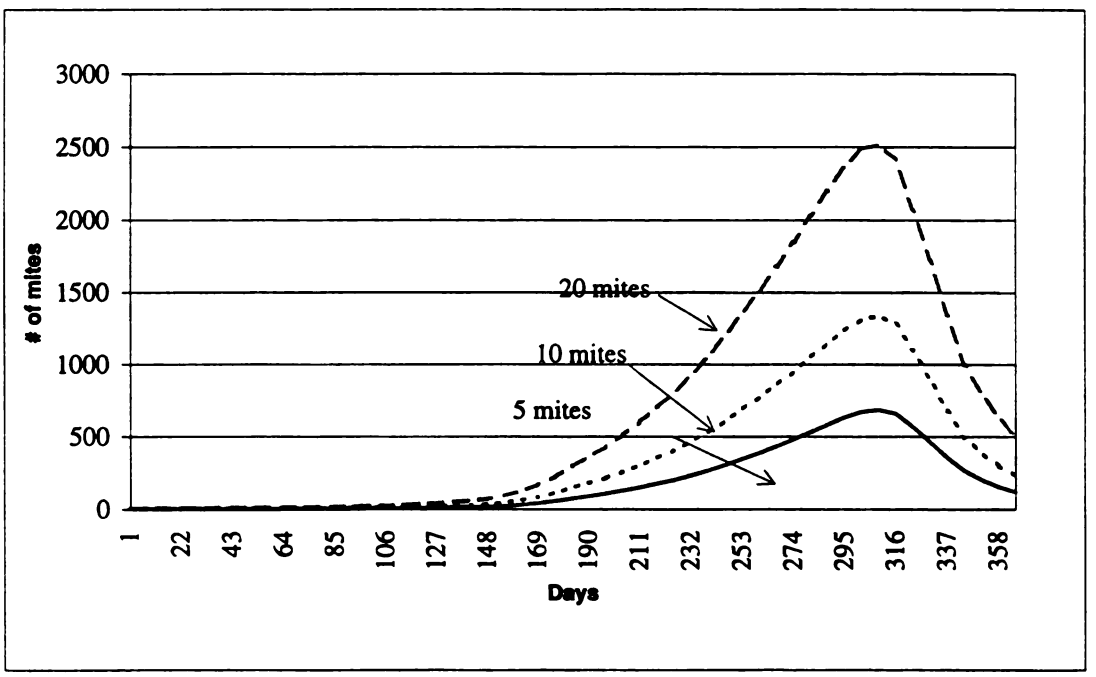

Figure 8. Mite population development in the first year when starting in April with different initial infestation.

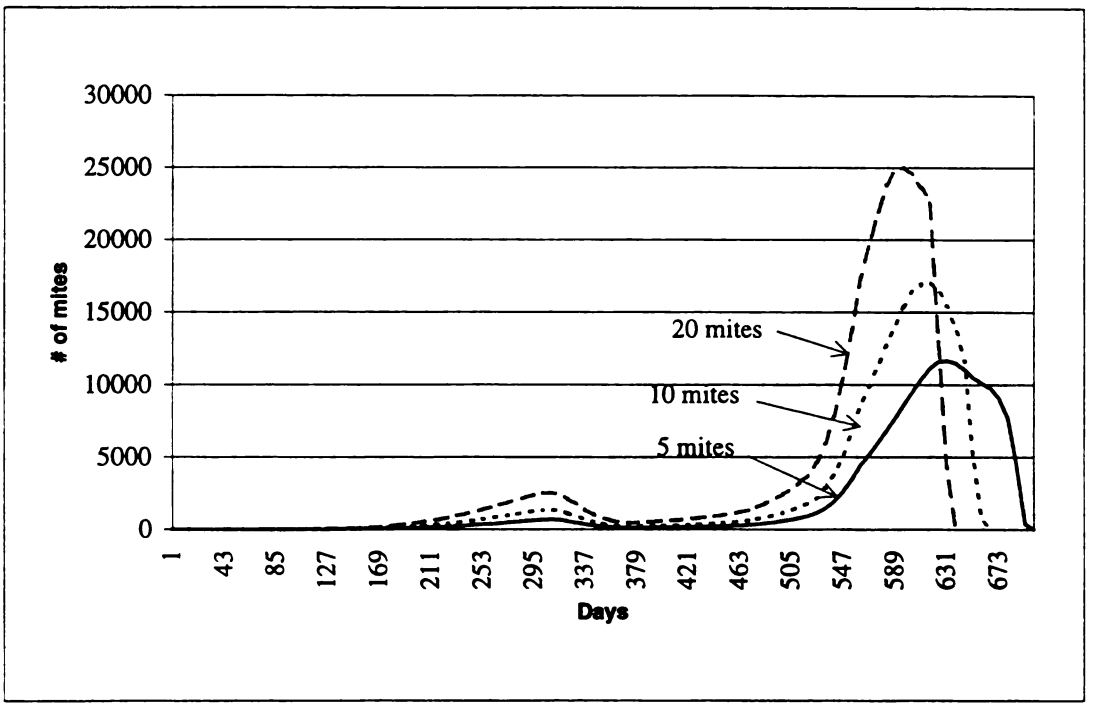

Figure 9. Comparison between mite population development when starting with different initial infestations in April until the collapse of the colony the second year.

Georgia were compare with mite population in North Carolina in North Carolina. They attributed the higher number in NC colonies to higher number of bees. Kraus and Page (1995) started with 50 mites at the end April and the mite population was up to 2,367 in October. And when started with 50 mites at the end of October, the mite population was up to 1,620 in April. They stated that the mite population increased up to 300 fold during one summer.

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USING MODEL SIMULATIONS TO PREDICT POPULATION RESPONSES IN HONEY BEES AND MITES BY INTRODUCING BIOLOGICAL CONTROL, CHEMICAL CONTROL, REINVASION, AND GENETICALLY MANIPULATED CHARACTER TRAITS INTO THE SYSTEM

ABSTRACT

Treatment efficiency and time of treatment were simulated in the honey bee and Varroa mite model and the results show that one chemical treatment is sufficient to control the mites for two years if there is no reinvasion from outside and if the beekeepers follow the label concerning length of treatment. However, reinvasion is inevitable in the field and that explains the failure of control measures and colony death even when treated once a year. This result shows how important it is for beekeepers to try to reduce reinvasion by cooperating with each other in the same area, by treating in the same season, and by including in their management decisions, practices that help in reducing drifting, robbing, swarming etc.

Controlling the mites by means of non-chemical measure is labor intensive, time consuming and is not practical for large operation beekeepers. However, some of the hobby and sideline beekeepers who have a few colonies and are willing to put in the effort, might find these techniques useful. Although, intensive drone removal reduces a high portion of the mite population, it still is not successful in controlling the mite population during the second year, when the population becomes high.

Trapping comb and hyperthermia techniques alone will not work for more than two years in high and moderately high population colonies. These techniques reduce the mite population significantly but not enough to control it.

The honey bee and Varroa mite model is used to evaluate some of the important mite and bee traits involved in resistance or tolerance of honey bees against Varroa colonies such as, grooming, brood removal, brood attractiveness, infertility of mites, post-capping period, and reproductive cycle.

The results obtained indicate that the model is a valuable tool for predicating the changes in mite and bee populations resulting from varying a single factor concerning the above mentioned traits. The values for these simulations were obtained from the research literature when available, or expert opinion when data was not available. The results from the model simulations illustrate the effect of these traits on the bee and mite populations and it shows that any thing that effects mite reproduction such as number of offspring, fertility, reproductive cycle and phoretic period are the most important traits for which to select.

INTRODUCTION

Modeling is an important tool that is used to predict the effect of some factors on mite populations and to show which factors have major effects. Studying of such factors in the field might take a long time and be costly. In addition, the model can consider the affect of these factors separately or simultaneously.

In the honey bee and Varroa mite model we attempt to show the effect of different control measures and the effect of reinfestation on mite population dynamics. In addition, we use the model to evaluate the effect of separate resistant traits on the population growth of

the mite and hopefully the model will clarify which resistance traits should be chosen for selection.

BIOLOGICAL AND CHEMICAL CONTROL AND THE EFFECT OF THE REINVASION ON MITE POPULATION DEVELOPMENT

Introduction

Controlling the mite population is necessary to keep the mite density under the economic threshold and prevent the death of bee colonies of European races. More than 145 pesticides have been tested and used for control of Varroa (Wienands, 1988). Pyrethroid Fluvalinate (Apistan), the most common acaricide that has been used to control Varroa all over the world, is the only one approved for controlling these mites in the United States. Reports about Varroa mites developing resistance to Apistan (Lodesani *et al.*, 1995) and the pesticide residues in honey and wax from Apistan and other registered products (Maria and De Paoli, 1994; Milani, 1994; Borneck and Merle, 1990; Hansen and Petersen, 1988; Barbina *et al.*, 1989) make it important to research alternative methods of reducing the mite population and limiting the use of acaricides inside the colonies.

Attempts have been made to control the mite population without using chemicals or with minimal use with various degrees of success. Although these methods are time consuming, labor intensive and may not be suitable for commercial beekeepers, those who do not want to use chemicals inside the hives, such as hobby and side line beekeepers may find these alternative methods useful.

Drone removal

Literature review. Varroa prefer drone brood to worker brood, proportionally drone cells are infested by approximately 12 times as many mites as worker cells (Calis *et al.*, 1996; Boot *et al.*, 1995). This preference can be utilized by beekeepers to use drone combs to trap Varroa.

The essence of this technique is the insertion of a drone comb or frame with drone foundation into the colonies and regularly remove the brood once it has been fully sealed. Schulz *et al.*, (1983) reported that drone comb removal was effective in controlling Varroa in lightly infested colonies, in heavily infested colonies it was only 15% better than the control and thus failed in slowing down the build up of the Varroa population. For this procedure to be effective, all drone brood present on any other comb in the colony must be cut out and removed (Weiss, 1984) otherwise mites may invade drone cells that are not removed from the colonies. Another way to do this is to cut and destroy all the drone sealed brood. Ritter *et al.* (1981) reported a 10% reduction of mite populations in both high and low infested colonies. Shilor (1980) reported a 54% reduction.

Lavagnino and Marletto (1996) periodically removed drone brood in two apiaries, cutting the drone brood 12.2 and 10.8 times. On average, the total number of mites removed averaged 1448 and 10303, receptively. In the second year the numbers were lower. Although this method was effective, it could be used for only a few months of the year, and by itself could not ensure colony survival.

Calis *et al.* (1996) reported that trapping mites in drone brood will be much more effective when it is applied during periods when no other brood is present in the colony, this will not allow the mites to escape by invading brood cells on other combs.

Boot *et al.* (1995) stated that trapping mites in drone brood can be an effective non-chemical method to control Varroa when it is applied during periods when no brood other than that introduced for trapping is present in the colony. They found that 462 drone cells are estimated to be sufficient to trap 95% of the mites in a colony of 1 Kg of bees.

Calis *et al.* (1996) designed a method to trap mites in drone cells which resulted in an overall effectiveness of 93%. In this study they used five pairs of colonies. One colony of each pair was made broodless. The brood was given to the other colony. This colony was split into a brood less part with the queen and a part in which a new queen was reared and which became broodless when all the old brood had emerged. This provided three times the optimal opportunity for trapping mites in drone brood, i.e., a broodless (part of a) colony.

Model Simulation. From the literature cited above, it is clear that there is a wide range of drone removal techniques attempted by researchers. Methods ranged from removing only a part of the drone brood to removing all the brood from the colony. The goal of this model simulation is to demonstrate the effect of drone brood removal on the mite population. The natural development of the mite and bee populations are shown in Figure 1. There was no attempt to remove the drone brood from this simulation. If the mite population is not controlled, then the bee colony will collapse after two years.

Then the simulations were run removing a range of drone brood. If one removed 99% of the drone brood after sealing, the simulation showed that the mite population will be reduced by more than 50% the first year (Figure 2). A 20%, 50% and 70% drone brood removal corresponded to a 9%, 30% and 42% mite reduction in the first year (Figure 2). However, the bee colony will still collapse during the winter of the second year or early in the spring of the third year (Figure 3) because of the buildup in the mite population during

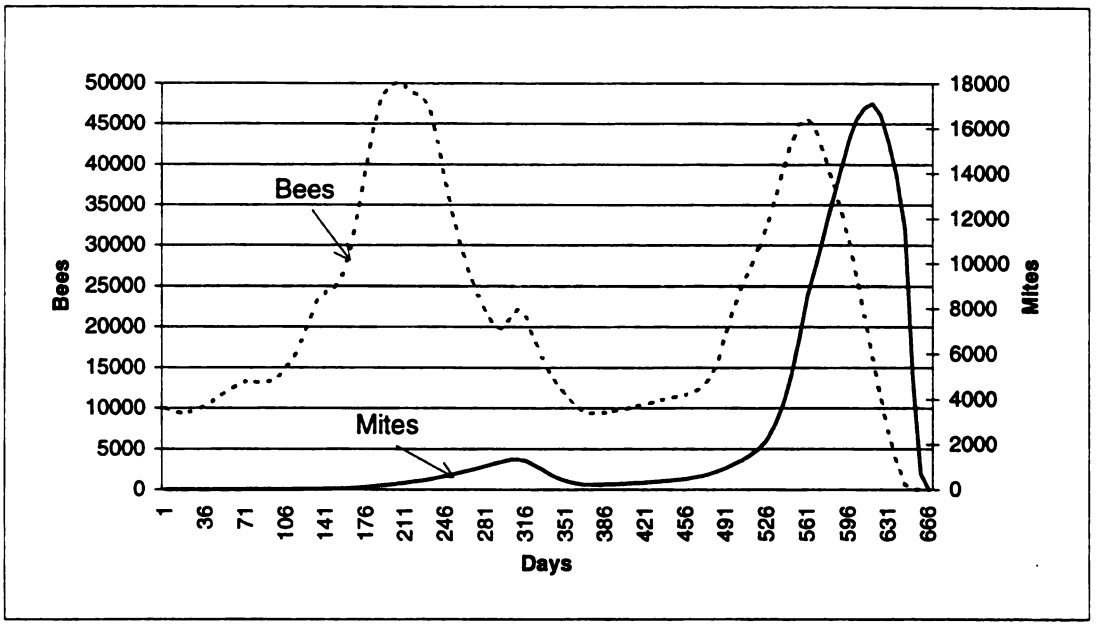


Figure 1. Mite and bee population development when starting with 10 mites in April and 10,000 adult bees in January until the colony collapses in the second year.

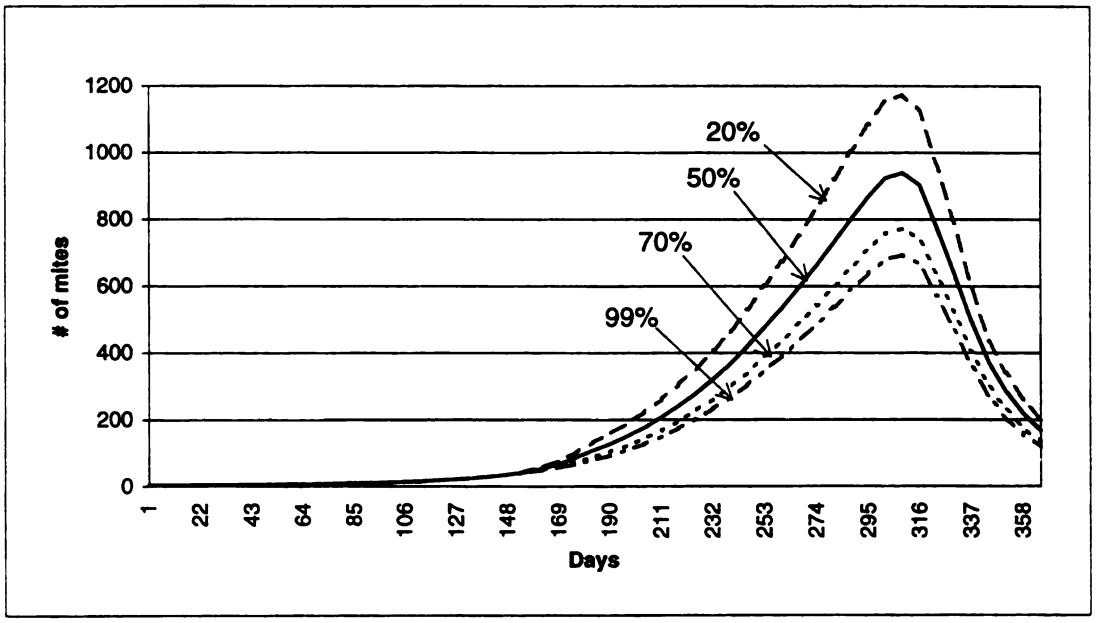


Figure 2. Mite population development in the first year when drone removal technique is used to control the mite population.

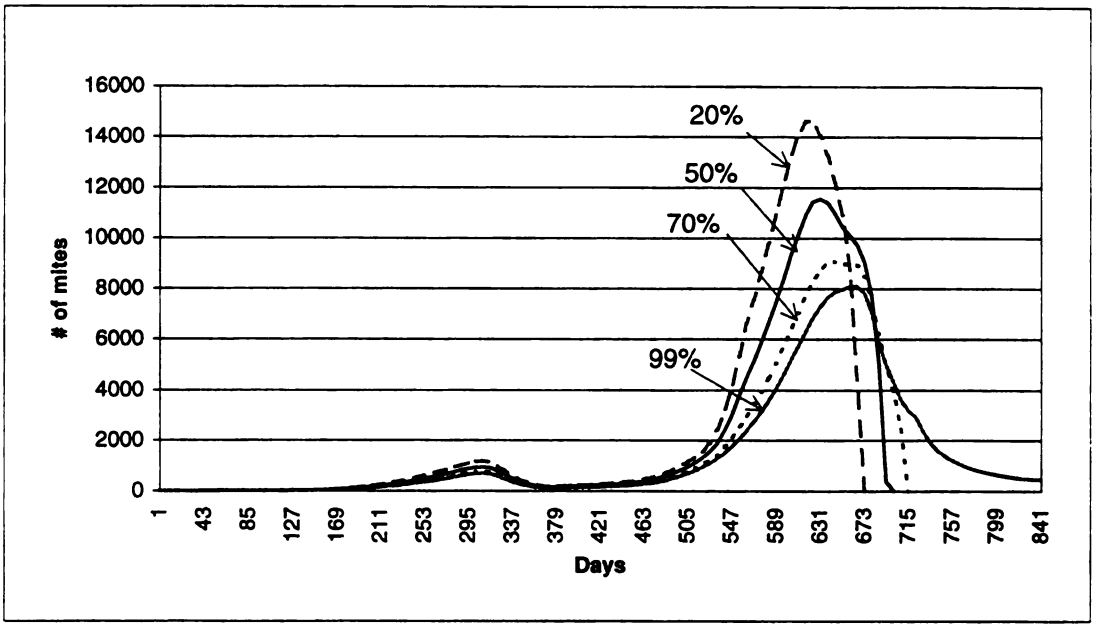


Figure 3. Mite population development when using drone removal technique to control the mite population: different percentages from the whole brood is removed during the whole season.

the second year. Hence, drone brood removal alone is not sufficient to control the mite population and it is necessary to use other methods of biological control along with drone brood removal.

Trapping comb technique

Literature review. In this method of biological control, the queen is confined to one comb, within a cage made of queen excluder. After a seven to nine day period, the queen is removed from the brood comb and placed on a new comb. After a total of 28 days, or 4 transfers, the queen is released and allowed to move freely (Maul, 1983). The combs are removed from the colonies after capping. Maul *et al.* (1988) recommended using trapping comb technique for 2 or 3 years, because mite levels continued to increase after that amount of time. Trapping comb technique gives an estimated reduction of 90% of the mites from infested colonies (Fries and Hansen, 1989; Maul and Klepsch, 1986; Rademacher and Geiseler, 1986).

There is some concern about colony survival without new bees, especially if the technique is applied for four successive cycles (28 days + 21 days = 49 days without new bees). Fries and Hansen (1993) reported if the sealed worker brood combs are destroyed, the bee colony will still be able to survive the winter. Their results demonstrated that it is possible to control Varroa using management methods only. However, they reported that the relatively high mite mortality during the third and fourth experimental year indicated that the use of the trapping comb technique by itself might not be sufficient for control of the mite in all colonies over a period of several years.

Camilla and Hansen (1994) showed that mite control using the trapping comb technique followed by heat treatment of the sealed brood for four hours at 44°C, combined

with drone brood removal, was sufficient to control Varroa infestations in most cases. However, they suggested that even for skillful beekeepers this control procedure can cause difficulties and as a solution, they suggested treating the colonies with a soft chemical after nectar flow, when trapping comb technique has not been successful carried out. In this procedure, the sealed worker brood was not destroyed but removed and treated with heat for four hours at 44° C and then returned to the colonies. Calis *et al.* (1993) suggested killing the mites trapped in capped worker brood outside the colonies with formic acid. They reported that 73.5 - 80% of the dead mites recovered from the colonies were from the treated brood cells.

Model Simulation. This model simulates the effect of the trapping comb technique on mite and bee populations. The simulation prevents the worker brood from emerging for 49 days and also examines the effect of applying the treatment at different dates to illustrate the impact that date of application will have on the mite and bee populations.

Two different times were chosen to apply this technique. The first time was early in the season, at the end of April (Figures 4, 6), and the second time was at the end of July or just after the peak of the adult population (Figures 5, 7). If one chooses to use this technique early in the season, then the number of mites remaining after the treatment will be significantly reduced, which will result in less mites after the peak of the drone and worker broods. The drawback of this time period is that the honey bee population will also be reduced by about 20% (going from 50,000 to 40,000), which will result in less honey production.

Using the technique later in the season has one major disadvantage in that the mite population will not be affected until it has already become high. After the treatment the mite

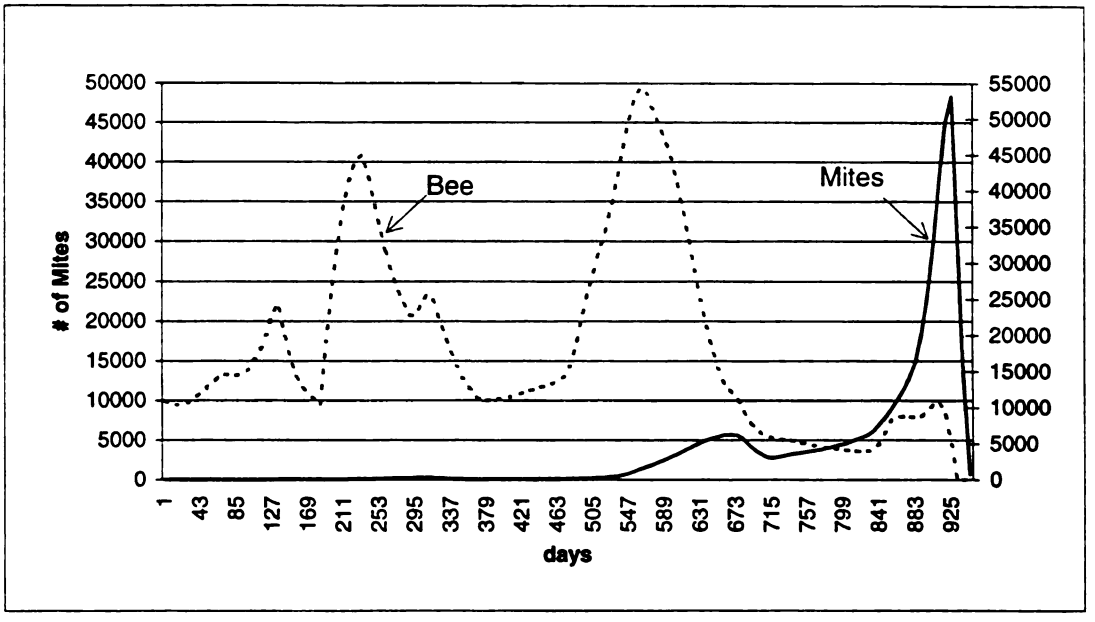


Figure 4. Mite and bee population development when using trapping comb technique at the end of April the first year to control Varroa population.

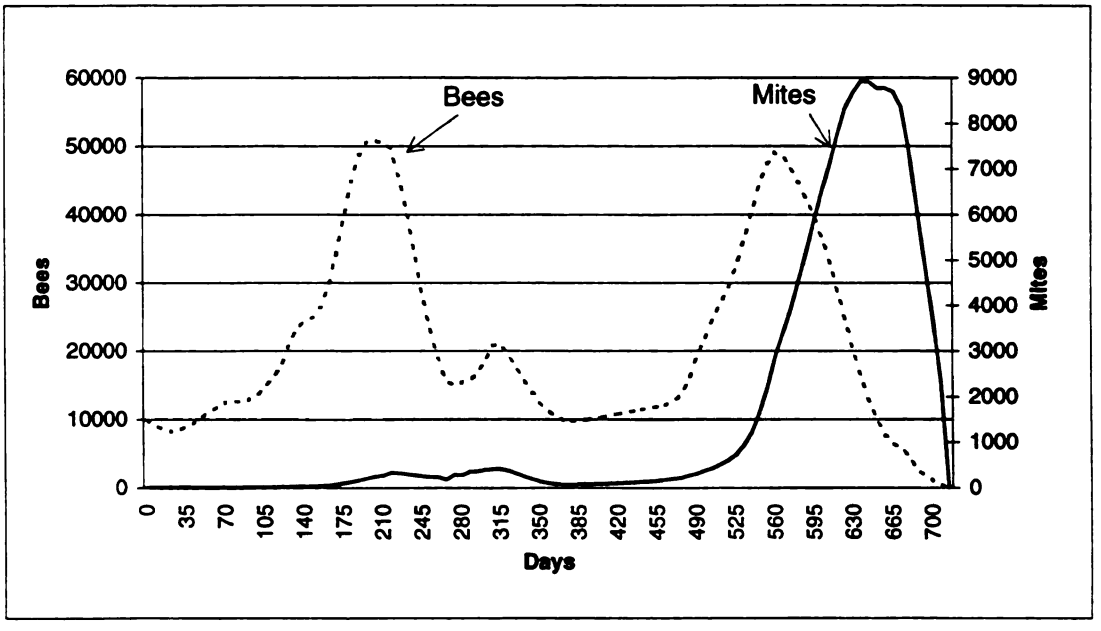


Figure 5. Mite and bee population development when using trapping comb technique at the end of July the first year to control mite populations.

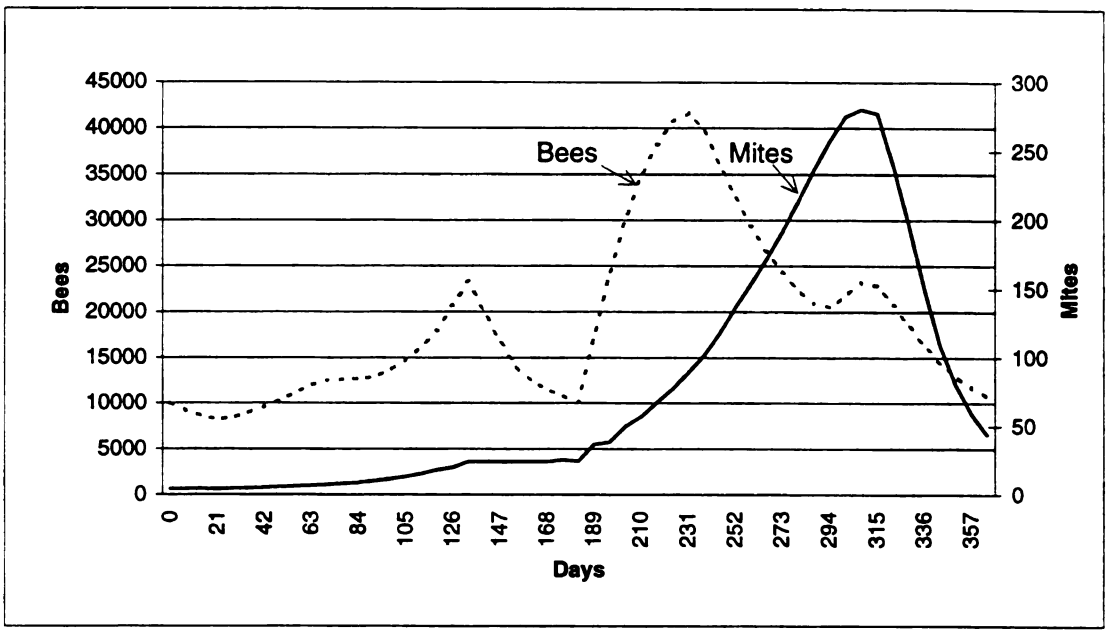


Figure 6. Mite and bee population development in the first year when using trapping comb technique at the end of April to control mite populations.

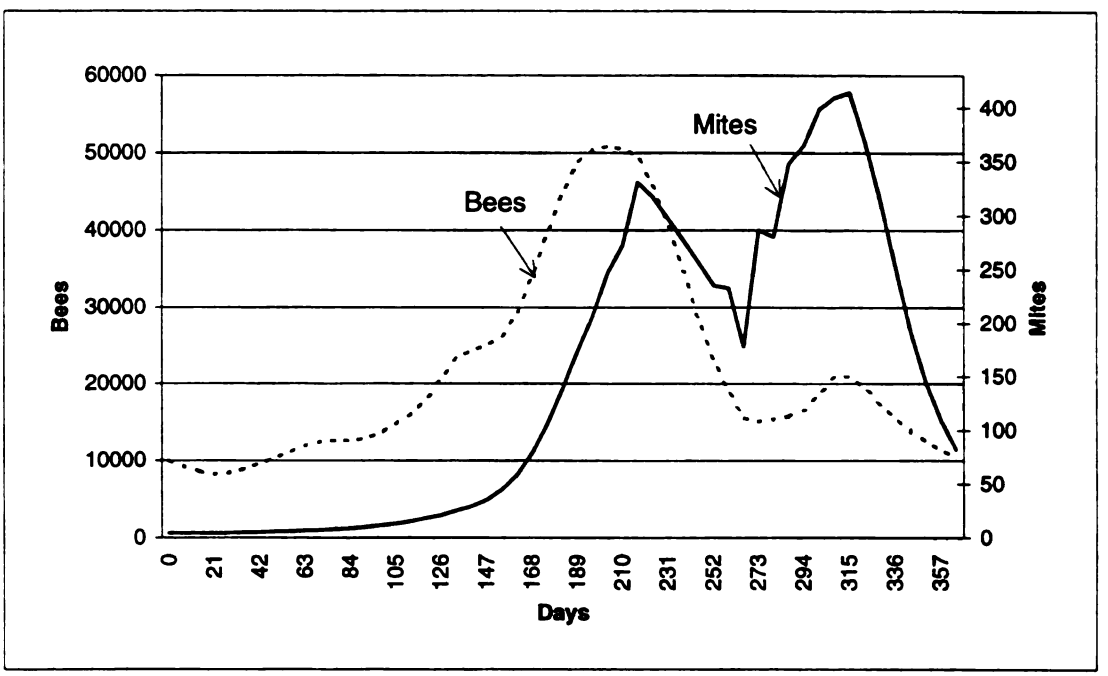


Figure 7. Mite and bee population development in the first year when using trapping comb technique at the end of July to control mite populations.

numbers will increase again because of the high number of mites entering the broods to multiply. The advantages of this time frame are that more honey will be produced because the honey bee population will also be greater. There will be more space available to store the honey. Also this technique might increase the number of foragers by shifting the workers duties from nursing to foraging.

This model estimates a mite population maximum of 1339 in the first year without using trapping comb technique (Figure 1). This number is reduced to 279 mites when using the technique at the end of April (Figure 6), and to approximately 418 mites when using it at the end of July (Figure 7).

The model can also be used to compare colony survival from the effect of treatment timing. The overall effect on colony survival shows that the colony actually survived longer when the mites were reduced early in the season because the overall mite population was less going into winter (Figure 6). The colony survived through the third year, although it was not healthy that third year. It collapsed immediately after the mite population drastically increased after the peak of the worker brood. When the trapping occurred at the end of July, the colony still collapsed in October of the second year (Figure 5). It collapsed early because the population was higher coming out of the first year of treatment.

The next step was to see the effect on the mites and the bee colony if the trap combs were used for two years. Both times of treatment allowed the colony to survive a third year when the trapping technique was used in two consecutive years (Figures 8, 9). The peak bee population was lower the first year with the earlier treatment, but both treatments resulted in a bee population ca. 50,000 during the second year. The colonies survived until June and July, respectively, the third year. They collapsed because of the high mite population

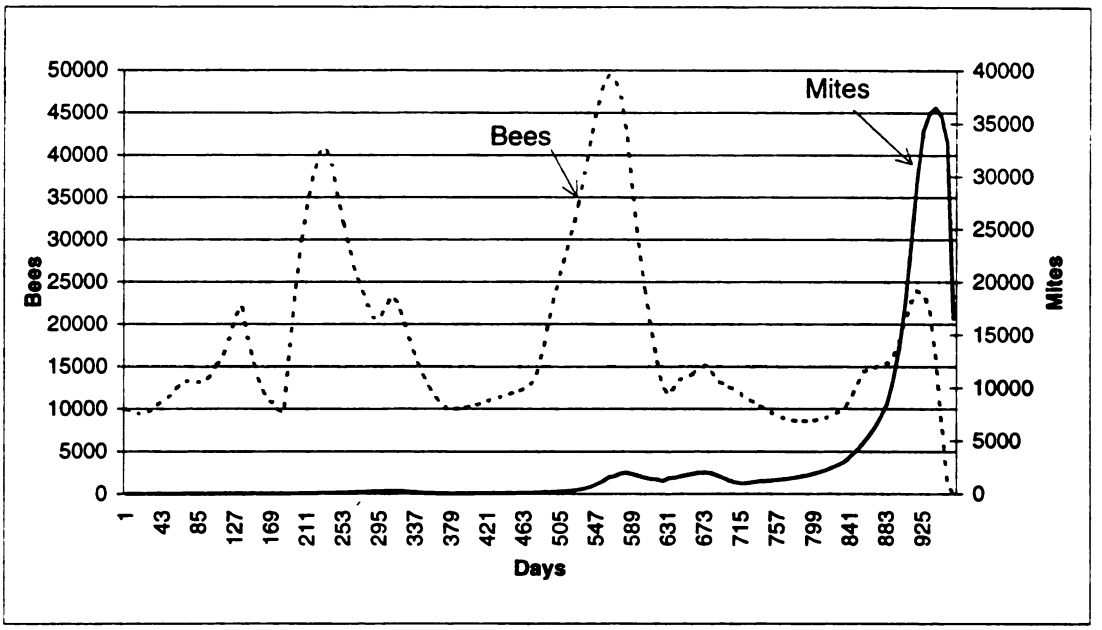


Figure 8. Mites and bee population development until the collapse of the colony when trapping comb technique is used in the end of April the first year and end of July the second year.

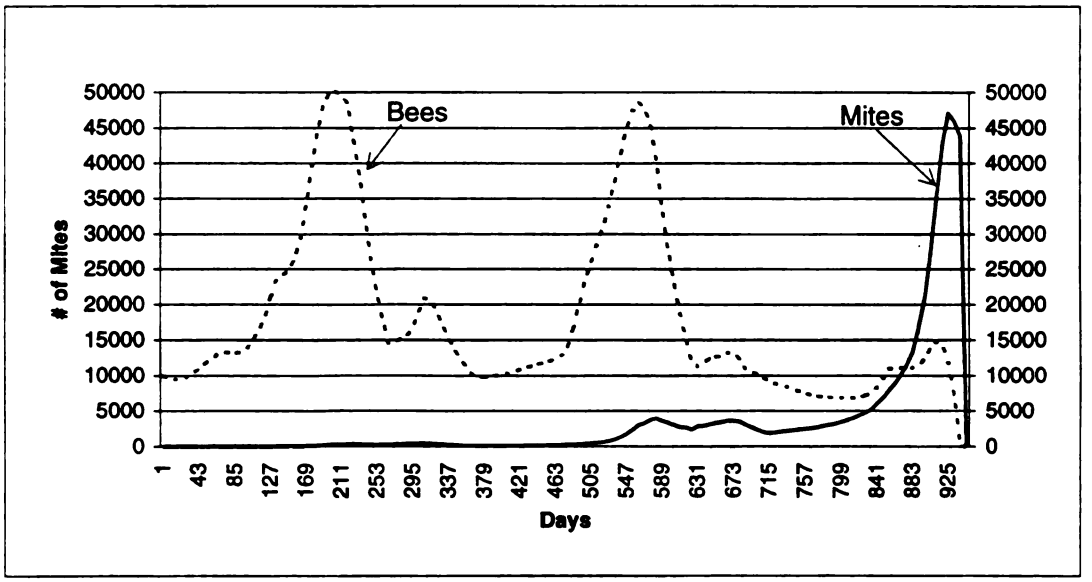


Figure 9. Mite and bee population development until the collapse of the colony when using trapping comb technique in the end of July the first year and end of July the second year.

following the brood peak during the third year. However, the technique was successful at removing about 60% of the mite population in the second year (Figure 10 & 11). The relatively high numbers of brood that are present in August and September allow the mite population to increase after the treatment.

The last model was used to simulate the effect of using the trapping comb technique for three years (Figure 12). It illustrates that the trapping comb is good at controlling the mite population for two years in highly infested colonies. With low infested colonies, it might work a bit longer. This result is in agreement with Maul (1988) who reported that the technique is good for 2 or 3 years, but reported that mite population levels continue to increase after that time frame. Fries *et al.* (1993) stated that the trapping comb technique might be insufficient for controlling mites in all colonies over a period of several years due to the high mortality during the third and fourth experimental year.

The next simulation used the two years of trapping comb technique combined with a third year of 99% drone removal. The colony still collapsed at the spring the third year (Figure 13).

Hyperthermia

Literature review. Varroa females are more sensitive to temperature above that of the normal honeybee brood nest level than are larval and pupal bees. Based on this slight difference in tolerance to heat, a heating method is used to eliminate Varroa (Rosenkranz, 1988). Rosenkranz (1987) exposed frames of brood without adhering bees to high temperatures in an effort to kill Varroa mites within the cells. Between 80-100% of adult Varroa females and 100% of the nymphal stage of the mite were killed in the broods that were exposed to 40C° (104°F) for 12h, to 44C° for 5h, or to 45°C (113 F) for 4h. when

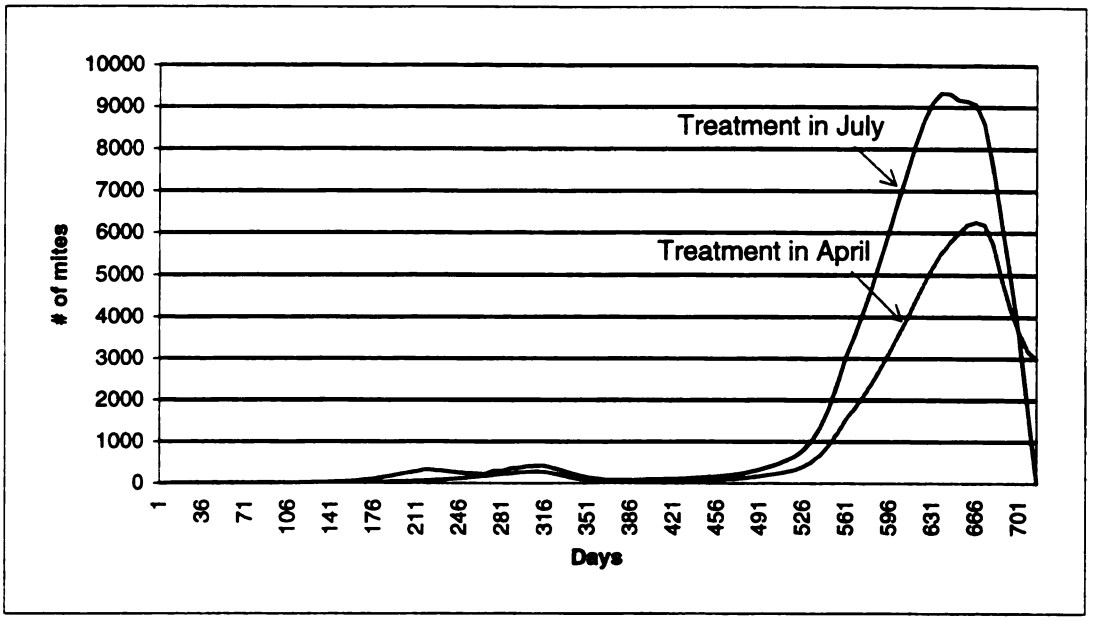


Figure 10. Mite population development showing the effect of trapping comb technique in first and second year.

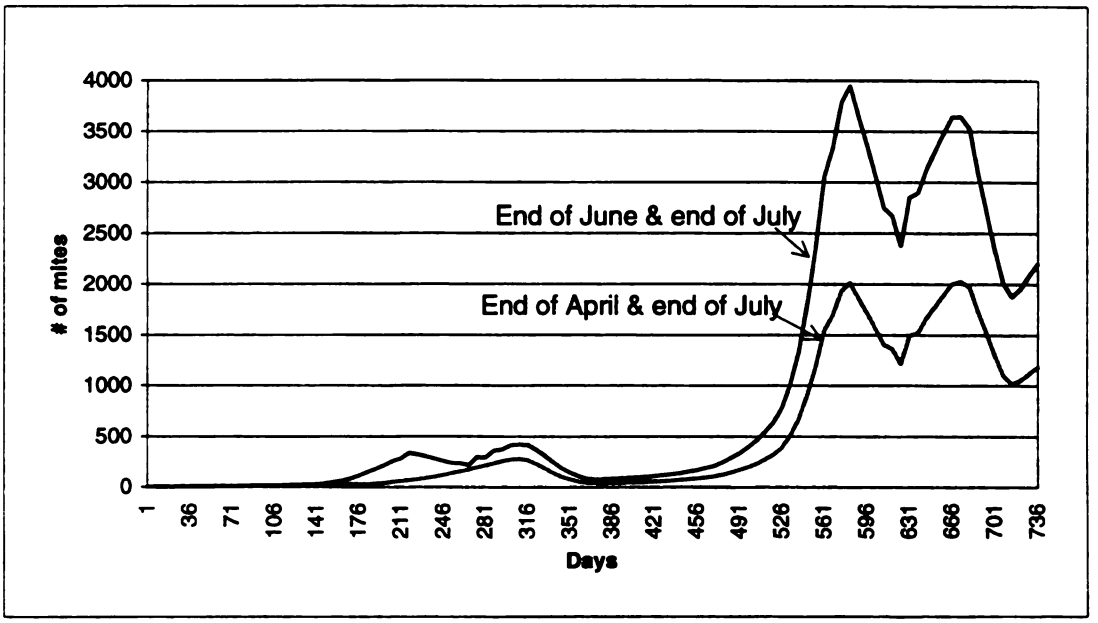


Figure 11. Mite populations for the first two years when using trapping comb technique in the end of April or the end of July the first year.

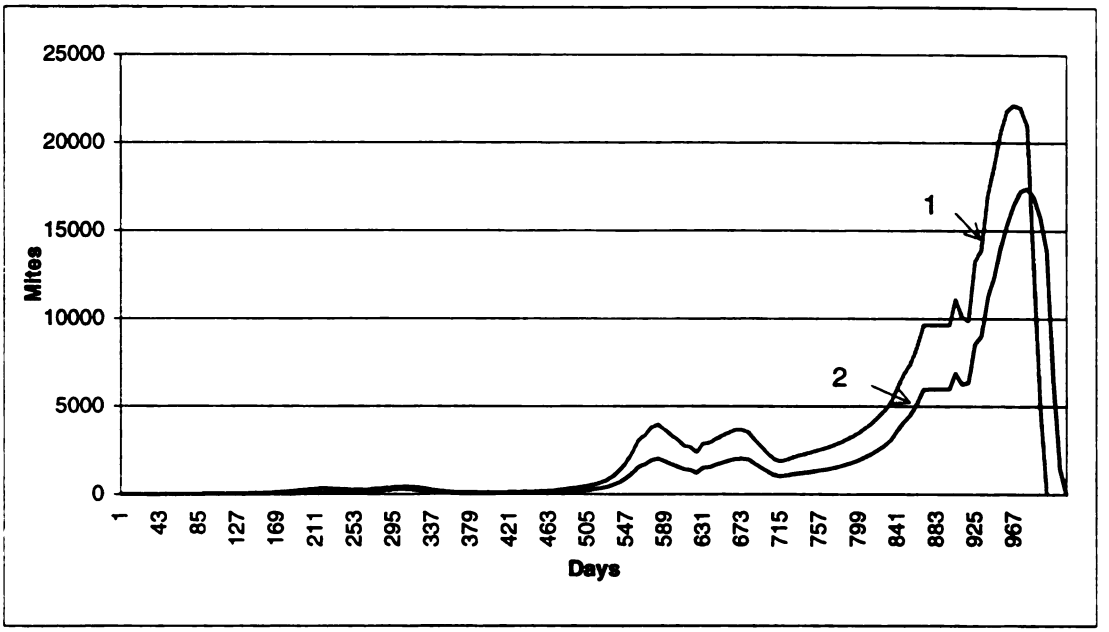


Figure 12.A comparison of mite populations when using the trapping comb technique for three years 1- end of April the first year & end of June the second year & end of April the third year 2- end of June the first year & end of June the second year & end of April the third year.

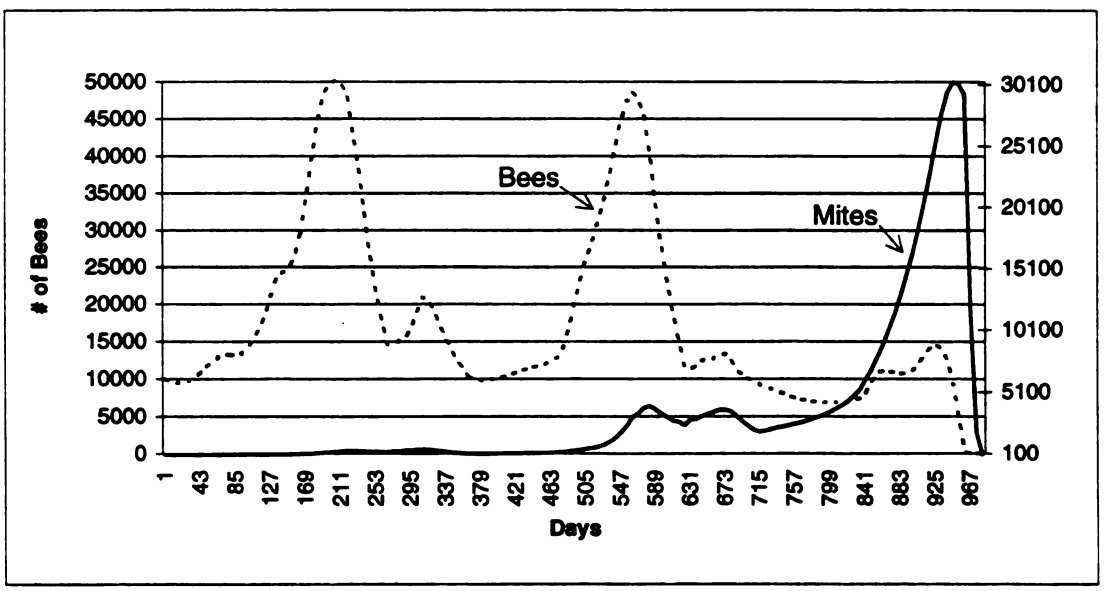


Figure 13. Mite and bee population development when using trapping comb technique in the end of July first year and end July second year and 99% drone removal in the third year

considering all stages of the brood comb, the maximum rate of damaged brood was about 5%, although the early stages were slightly more sensitive to the high heat. Appel and Buchler (1991) found similar success when the brood was heated in an incubator shortly before the emergence of the bees, 100% of the mites were killed after at least 4h treatment with 44C°. They recommend heat-treatment for trapping combs when there is precision in controlling temperature and heat regulation.

Engels (1994) stated that hyperthermia was 100% effective, about one day after the treatment all adult female mites together with the nymphs were found dead in the capped brood cells. According to the amount of capped brood present in the colony, with one hyperthermia application between 50% and 80% of the total mite population in a hive can be eliminated. Hoppe and Ritter (1986) applied thermal therapy in the field using 6 artificial swarms of normal size (ca. 15,000 bees). The swarms were treated at 48°C for 20 minutes and 6 others at 50°C for 15 minutes. In comparison to the controls, an average of only 23 and 38% of the mites, respectively, were killed. The low mite mortality is due to the strong tendency of the bees to reduce the temperature by cooling and heavy ventilation (Engels and Rosenkranz, 1992; Hoppe and Ritter, 1986). Therefore, hyperthermia of capped brood frames outside the hive remains the only applicable method .

Model Simulation. This is different from the previous two control strategies because the brood will not be damaged and the bees will emerge inside the colony. The model predicts an approximate 50% reduction in the mite population (Figures 14, 15). The simulation shows the differences in mite populations in the first year when no control was used, and when the hyperthermia was 90% and 100% effective (Figure 14). The colony collapsed sooner with 90% efficiency than with 100% (Figure 15). The results, once again,

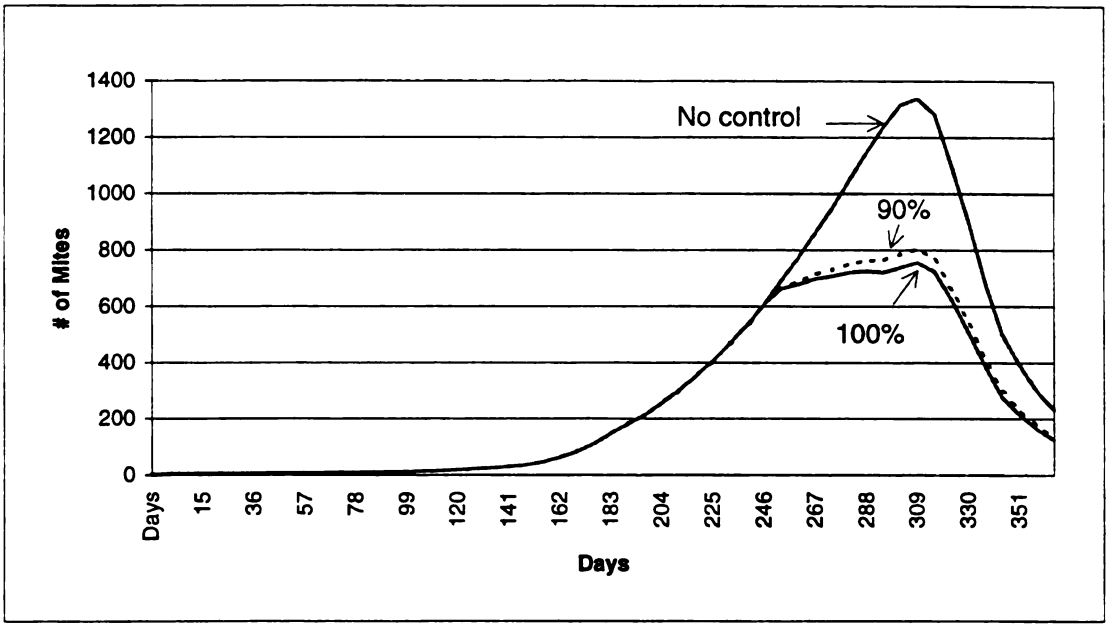


Figure 14. Comparison between mite populations in the first year with and without hyperthermic control.

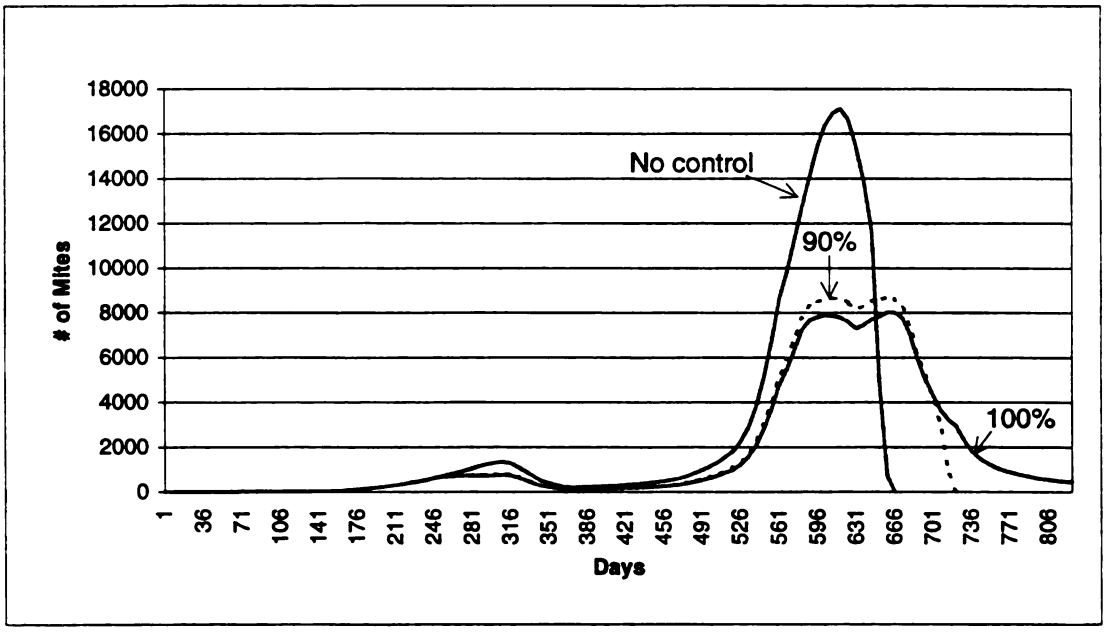


Figure 15. Mite population development until the collapse of the colony when hyperthermic technique is used to control the mite population.

indicate that this single biological control mechanism is not sufficient to control the mite population alone.

Chemical control

Literature review. More than 145 pesticides have been tested and used for control of Varroa (Wienands, 1988). Pyrethroid Fluvalinate (Apistan), the most common acaricide that has been used to control Varroa all over the world, is the only one approved for controlling these mites in the United States. Efficacy of Apistan generally ranges from 98-100% (Hillesheim *et al.*, 1996). Reports about Varroa mite developing resistance to Apistan (Lodesani *et al.*, 1995) and the pesticide residues in honey and wax from Apistan and other registered products (Maria and De Paoli, 1994; Milani, 1994; Borneck and Merle, 1990; Hansen and Petersen, 1988; Barbina *et al.*, 1989). By using the model simulation, we attempt to illustrate when the most effective time to treat and to show the effect of different doses and length of treatments.

Model simulation. The model can be used to simulate the effect of chemical control on mite population dynamics. This model assumes there is no reinvasion from outside. Two different efficacy rates were chosen, 70 and 90%. If a chemical control is used for 65 days and is only 70% effective it will control the mite population for three years and the colony will collapse after the brood peak in the fourth year, if not treated again (Figure 16). Similar effects were found when the control was 90% effective (Figure 17); although, the mite population was considerably lower at its last peak.

If chemotherapy is used, with an efficacy of 99%, for seven days the mite population is reduced by about 50% to a peak of ca. 625 the first year (Figure 18); but the colony will still collapse at the end of the second year (Figure 19). The mites that were in sealed cells

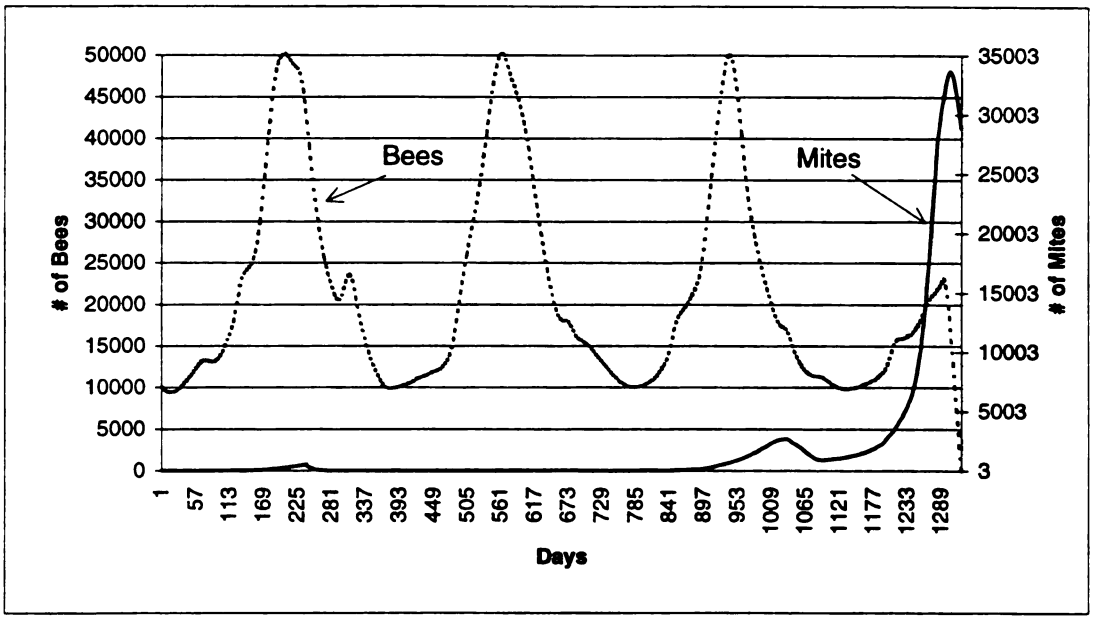


Figure 16. Mite and bee populations when using chemical control with 70% efficacy at the end of August for 65 days.

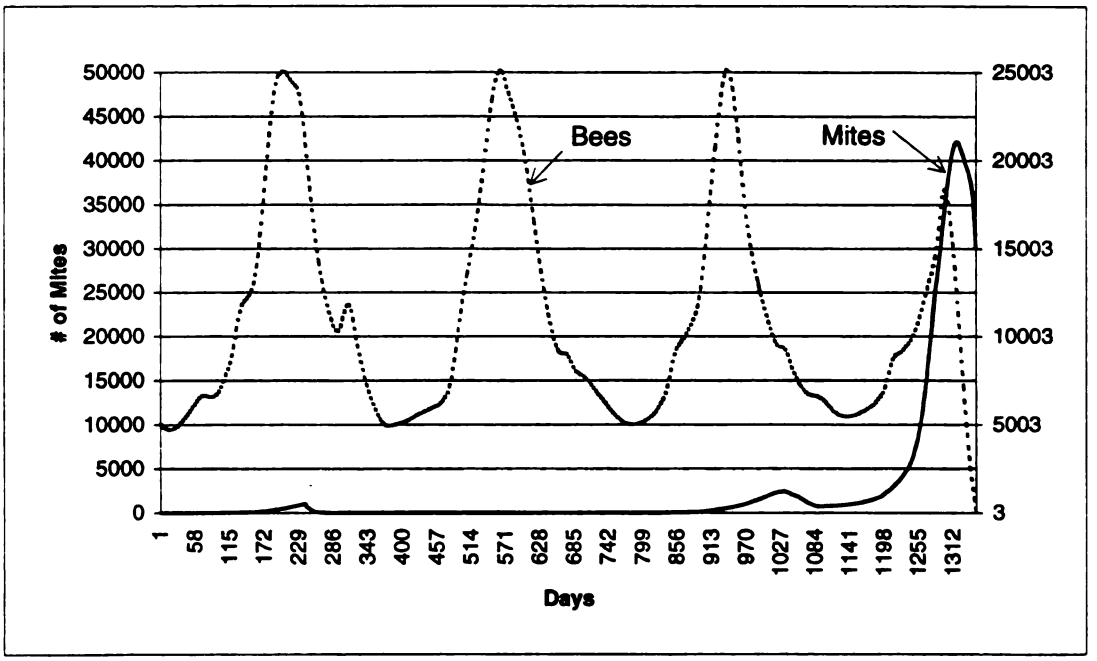


Figure 17. Mite and bee populations when using chemical control with 90% efficacy at the end of August for 65 days.

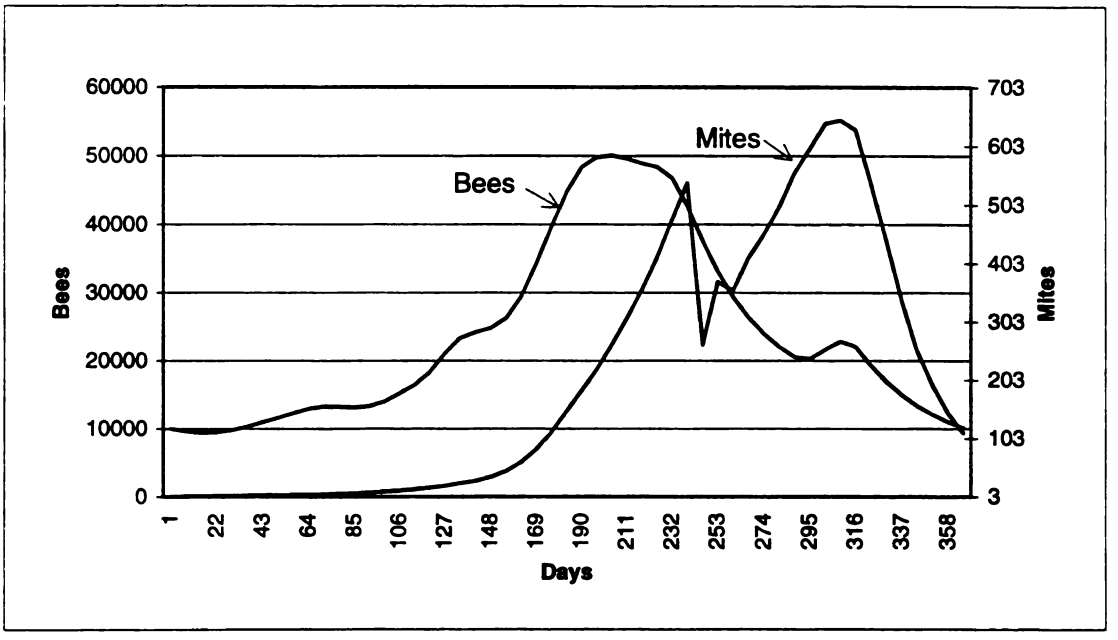
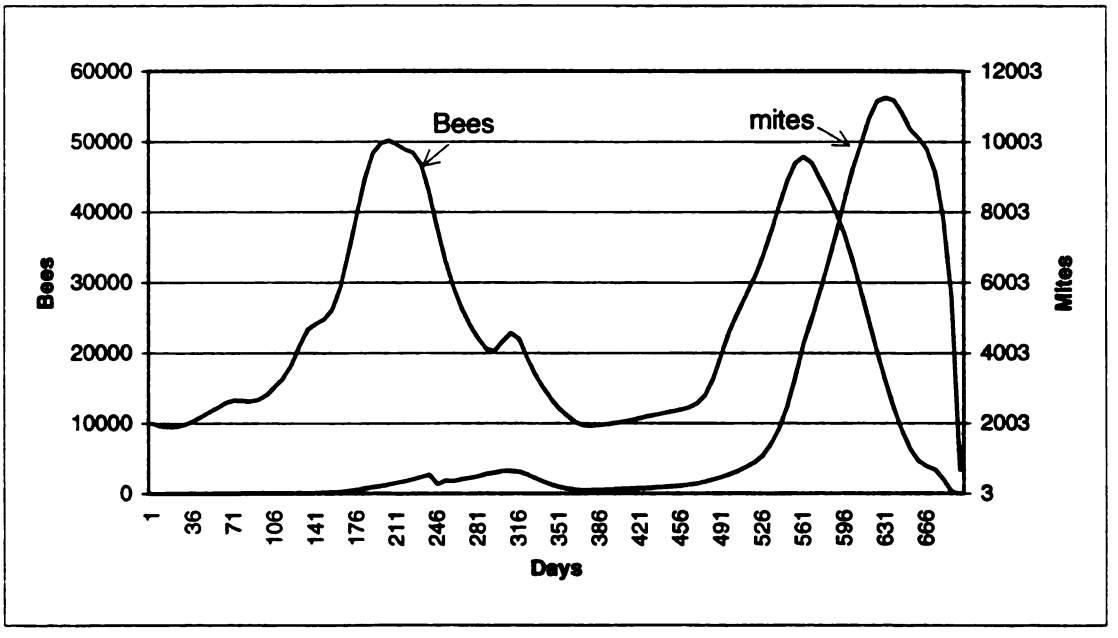


Figure 18.Mite and bee populations in one year when using chemical control with 99% efficacy in the end of July for 7 days only.



Figures 19. Mite and bee populations until the collapse of the colony when using chemical control with 99% efficacy at the end of August for 7 days only.

during the treatment were not effected by the treatment and were left to multiply after leaving the cells. The colony collapsed in October the second year because seven days was an insufficient length of time for control. When treatment lasted for 14 days (Figure 20) the effect on mite population will be greater and the colony will survive until the brood peaked in the spring the third year.

Reinfestation

Literature review. If a large number of colonies are highly infested within the flight radius, the mite population can increase in five months from zero to an average of 6000 mites per colony according to an investigation by Ritter (1986). In comparison, the increase in infested colonies with little invasion pressure remains small during the same time period. A maximum of 2000 mites was found in the colonies in the fall. Greatti *et al.* (1992); Milani *et al.* (1993) reported that the daily reinfestation rate in highly density areas with honey bees was low during spring, varied between 1.6-13.7 mites/day/colony during June, July and first week of August, and rose during September and October up to 100 (on average, 31.6) mites/day/colony; it was relatively high when nectar was scarce. Drones were prevented from entering the colonies by means of queen excludes.

Imdore and Kilchenmann (1994) found that, numbers of mites started to increase in the monitored colonies (they were free of mites) at one apiary in June when infested colonies in a neighboring apiary started to die. Robbing of the weakened (infested) colonies was observed. It is concluded that mites were carried by robber bees back to the healthy colonies; number of mites transported is estimated as 3000-4000 mites/colony.

The zone within a radius 7 km a round the center of an infested apiary is considered contaminated. The zone within a radius of 100 km (double of the flight range of swarm) is

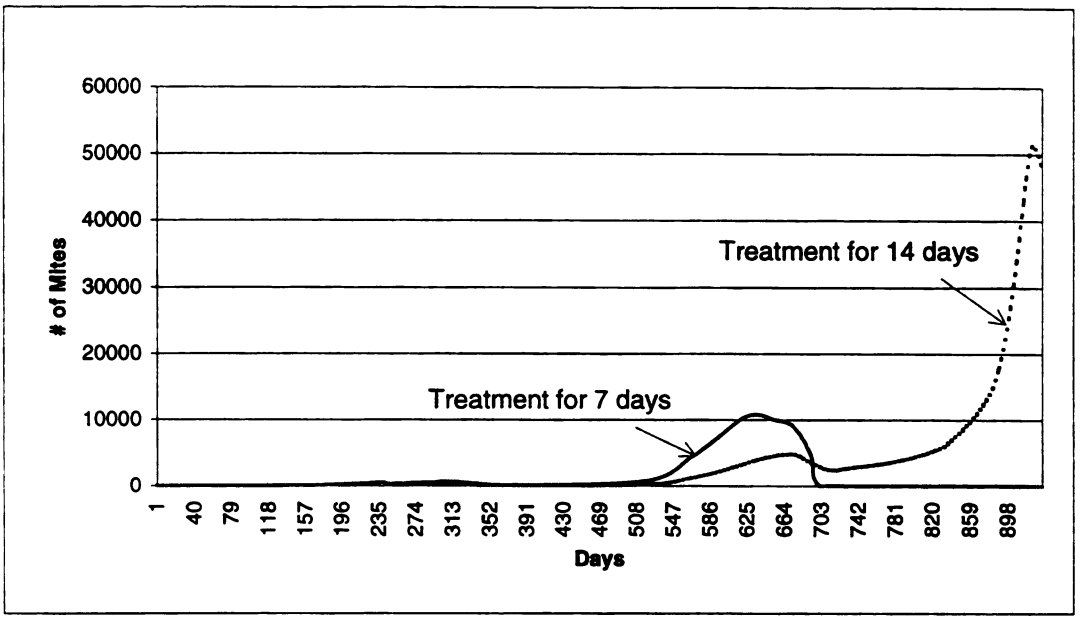


Figure 20.Comparison of mite populations when using chemical control in the end of August with 95% efficiency for 7 or 14 days.

considered exposed (Sulimanovc, 1984). As one colony of bees reaches the point of total collapse, the few bees that leave the hive carry 10 or more mites each, and fly to neighboring colonies or apiaries (Mussen, 1993). Foraging bees also carry the mites. In foraging bees the infestation increased from 0.2% in April to 21-32% in October, and in some colonies the level of infestation of foraging bees increased 20-25 times (Artemenko *et al.*, 1978). Huttinger *et al.* (1981) report that 5.2% of the flying drones were infested and 6.1% of the drones caught at the congregation area, while only 3.9% of the flying foragers and 0.7% of water-carrying bees. Huttinger and Pechhacker (1988) observed a mean of 4.5 foragers drifting in a day from each of three colonies 10-80 m apart, and even fewer bees drifted from more distant colonies. Sulimanovic (1984) found that 6% of the bees drifted to another bee hive in a stationary apiary, and in a migratory apiary the number of drifting bees increased to 18%.

Marked drones have been found 8 miles from their home apiary, and some researchers indicate that 23% of the Varroa mites outside cells may be on flying drones, while 17-20% of the young bees of nursing age carried Varroa mites (Mobus and Connor, 1988). Currie and Jay (1992) found that 47% of the drones drifted from their parent colonies, and 21% of those drones drifted more than once. The proportion of drones that drifted decrease with increased spacing between colonies, but only at the longer distance. Although 30-60% of drones drifted to colonies up to 50m away, only 20% of the drones drifted to colonies that were 100m away. However, the workers drifting was 44.3%, 26.3%, and 12.6% when the distance between hives was 3, 6, and 9 m respectively (Jay, 1966).

Filipov (1978) found that infestation spread in 32 days within a 100 m radius, in 73 days within a 500 m radius, and in three months within a 6-11 km radius depending on the

density. Gandinger (1985) estimated that the spread from apiary to apiary was about 3.5 km/yr. Natural progression occurs at the rate of 30-40 km annually (Robaux, 1988). Ritter and Leclercq (1987) reported that the risk of infestation can be reduced only by treating all colonies in an area in the same season.

Model Simulation. The model can also be used to simulate the impact of reinvasion on mite population dynamics (Figure 21). Geratti *et al.* (1992) estimated reinvasion patterns for one year. They estimated that 2.4 mites per day reinvaded in June, 4.7 in July, 5.9 in August, 31.6 in September and October, and 2.4 in November. Thus, the mite population can increase by about 4,000 mites as a result of reinvasion pattern. According to Ritter (1996), if there is a large number of colonies infested within flight radius, the mite population can increase from undetectable levels to an average of 6000 mites in a five month period.

Figure (22) illustrates the difference in mite populations when there is no reinvasion compared to one where 300 mites were introduced by robber bees on one day at the end of August. Hence, the results presented here show the important role that reinvasion plays in treatment protocol and on the outcome of research results when studying mite population dynamics in the field.

SELECTION TOWARD VARROATOSIS RESISTANCE

Introduction

Selection toward varroatosis resistant or tolerant strains has become a major issue in practical honey bee breeding (Koeniger and Fuchs, 1988; Kulincevic and Rinderer, 1988; Otten, 1990; Mortiz and Jordan, 1992; Buchler, 1994). In a comprehensive review, Buchler (1994) outlined the current scientific findings in colony defense mechanisms . Boot *et al.*

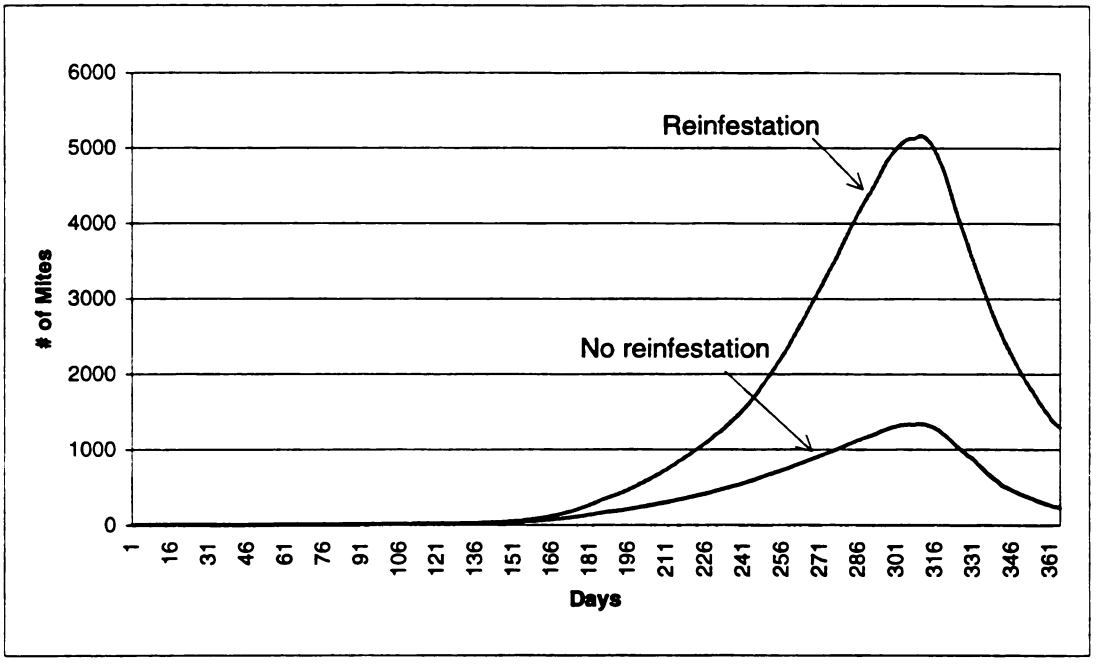


Figure 21. Mite population development in the first year with and without reinfestation.

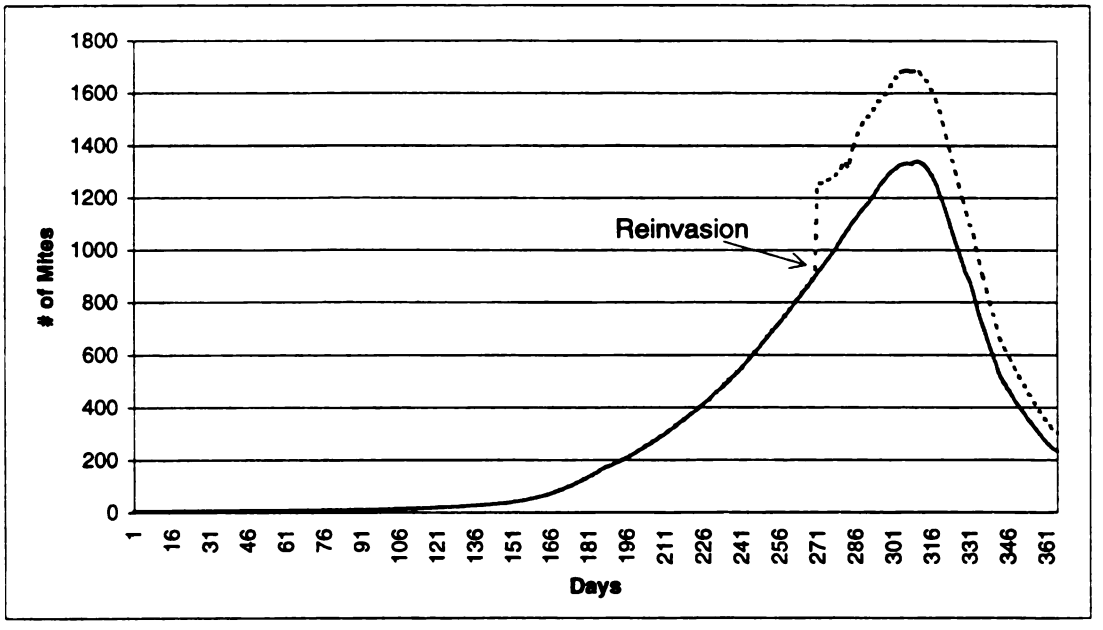


Figure 22. Mite population development without re invasion or when 300 mites are introduced in one day by robber bees at the end of August.

(1994) and Buchler (1994) listed the important traits involved in resistance of honey bees against Varroa colonies, namely, grooming, brood removal, brood attractiveness, infertility of mites, and post-capping period.

In these model simulations we attempted to evaluate some of the resistance traits mentioned above and to compare the results between some of the published parameters to see their effects on the mite population dynamics.

Grooming and hygienic behavior

Literature review. In the Asiatic honeybee *Apis cerana* F, the original host of *V. jacobsoni*, the infestation rate remains at low levels and the parasite does not severely harm the colony, and that may be due to the number of defense mechanisms that these bees have developed. One of these mechanisms, as described by Peng *et al.* (1987), is the active removal of adult mites from the bodies of worker bees. This process involves self-cleaning behavior. After showing signs of irritation, the bee performs a grooming dance, and then nestmate cleaning and group cleaning behavior occur. This resulted in removing (within two hours) more than 99% of mites added to colonies. Only 0.3% of the mites were removed by grooming in colonies of *A. mellifera.* Buchler *et al.* (1992) also compared grooming in *A. cerana* and *A. mellifera* and found successful mite removal in 75% of the cases in *A. cerana.* In *A. mellifera*, 48% of the mites were removed by grooming. Fries *et al.* (1996) reported lower numbers in full-sized colonies of *A. cerana*, 56% of 220 mites were removed by the bees in 6h and, of those, 30% were damaged; results for *A. mellifera* colonies were 21% of 280 mites and12%, respectively.

Ruttner and Hanel (1992) examined the natural mortality of five *A. m. carnica*

colonies for about one year and found on average 26% of the mites collected from inserts showed injuries to the legs but rarely to the cuticle of the idiosoma. Moretto *et al.* (1991) reported that 5.75% of the mites were removed by *A. m. ligustica* bees within 30 min after infestation, and an average of 38% (ranging from 10-70%) were removed by Africanized hybrids of *A. mellifera* bees.

Hygienic behavior of bees was described by Rothenbuhler (1964) in relation to resistance against American foulbrood (*Bacillus larvae*). The hygienic behavior of bees against Varroa mites was observed in both *A. cerana* and *A. mellifera*. Rath and Drescher (1990) showed that the detection, uncapping, and removal of Varroa-infested worker brood cells by the *A. cerana* worker, artificially-infested worker brood cells were removed to 98% within 5 days. Boecking and Drescher (1990) reported that artificially infested worker brood cells were detected, uncapped and removed to various degrees and they showed that brood cells infested with one Varroa mite were rejected from 14.3 to 95.8% of the time. Those with two Varroa from 25.0 to 100% were found after ten days. Boecking and Drescher (1991) reported that the removal of brood cells infested with one mite in *A.m. carnica* was 5.5% (minimum) up to 95.8 (maximum.). Within the same colonies, brood cells infested with two Varroa mites showed a removal rate from 4.8% (minimum) to 100.0% (maximum). In another study, Boecking and Drescher (1992) reported the removal rate was 24-41% of cells containing 1-2 mother mites after 10 days. Removal rates 15.4% versus 10.9%; 2mite/cell: removal rates 41.9% verses it was found that the rate was higher from other colonies, 32.2% (Boecking and Drescher (1994). Boecking and Ritter (1993) found workers in 15 test *A. m. intermissa* colonies detected and removed up to 75% of artificially infested brood and

removed up to 97-99% of freeze-killed brood in each of two trials.

Moosbeckhfer (1992) reported a significant negative correlation between the number of damaged mites found in the period between August/September, and the infestation of brood and bee samples and the total infestation found in a field test with 111 colonies.

Model Simulation. The model was used to simulate the effect of hygienic behavior on the overall mite population. When workers opened the infested cells, some of the mothers will be killed (Boecking and Drescher, 1991); but, more importantly, the most serious impact will be on the reduction in offspring. Figure 23 illustrates the impact of a 5, 3, and 1% reduction of number of offspring in worker and drone cells, as a result of cell uncapping by workers, on the overall mite population.

Infertility and fecundity

Literature review. Koeniger *et al.* (1981 ; Anderson,1994) reported that *Varroa jacobsoni* does not normally reproduce when it infests worker brood of the Eastern honey bee, *Apis cerana*, extensive mite reproduction occurs only on drone brood. In *A. mellifera* only a portion of the Varroa mites do not reproduce. Blum (1989) reported mite reproduction rates in worker cells at 88.7%, Fuchs and Langenbauch (1989) recorded 92.7% and Buchler (1990) found 86.6% reproduction in worker brood cells. Sulimanovic *et al.* (1982), Schultz (1984), Mossbeckhofer *et al.* (1988), Ifantidis (1990) and Boot et al. (1995) reported infertility rates in worker cells of 13, 16, 7, and 8-12% respectively. In drone cells, Fuchs and Langenbach (1989), Ifantidis (1984), and Schultz (1984) also found lower levels of infertility in drone cells. They reported 8, 4, and 5%, respectively. Ritter and De Jong (1984) observed only 43% of the mites in *A.m. ligustica* in worker cells in South America to be

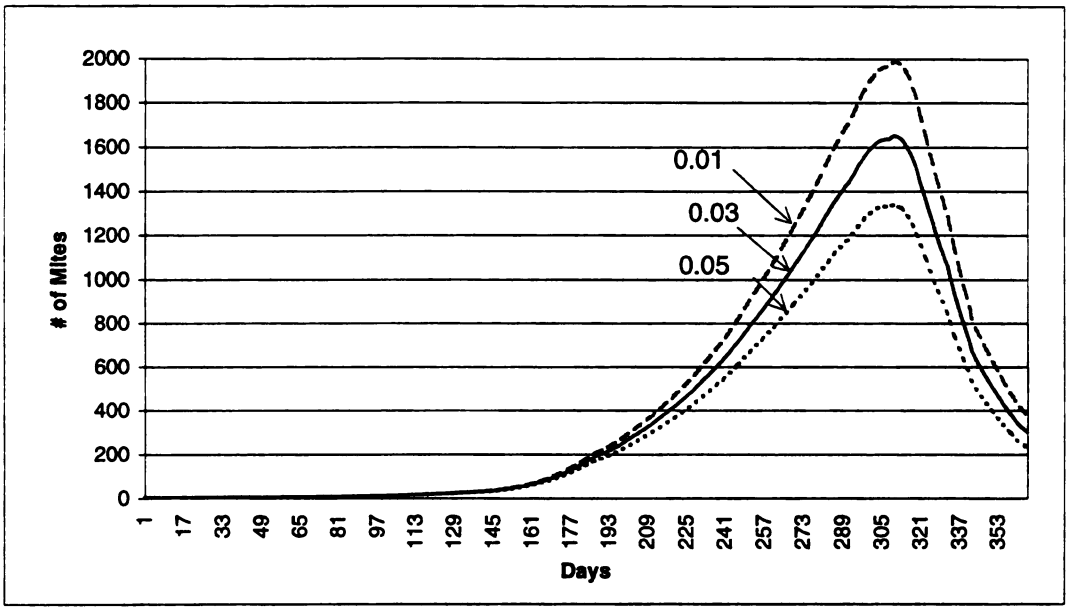


Figure 23. Mite populations in the first year when starting with 10 mites in April and when having different percentages reduction of offspring per worker and drone cell as the result of hygienic behavior.

fertile. Marcangeli *et al.* (1992) estimated that, depending on season, between 56% and 72% of the mites in *A. m. ligustica* colonies were fertile. Rosenkranz and Engels (1994) compared Africanized and European colonies of *A. mellifera*, and found less than 40% of females mites were fertile in Africanized bees, whereas, in European bees between 80-90% were fertile. In another study by Aumeier *et al.* (1996) the percentage of infertile mites was 49% in Africanized bees comparing to only 17% in carnica colonies.

Ritter and De Jong (1984) found that in tropical Brazil fewer (25-60%) female mites reproduce when entering brood cells than in Germany and Turkey where the rate was about 80%. Camazine (1986) reported that in European bee colonies in Brazil, 75% of infested brood cells have immature mites compared with only 49% of infested brood cells in colonies of Africanized bees.

Ruttner (1984) reported that colonies in Uruguay could resist Varroa infestation without any treatment; this was attributed to the very low fertility rate (10-30%) of the mites in worker cells. In Tunisia, Ritter (1990) reported that comparatively low numbers of fertile mites reproduced (50-80%). This demonstrates the increased tolerance of *A. m. intermissa* to Varroa.

The number of offspring produced by each mother Varroa mite entering the brood cell is an important factor effecting the mite population, those numbers depend on the type of brood they are, whether it is worker or drone cells. Schulz (1984) measured offspring production by fertile female mites in worker brood as 1.8 (including infertile mites 1.6) and drone cells the reproductive factor was 2.7. Fuchs and Schultz (1984), Ifantidis (1984), Fuchs and Langebach (1989), and Martin (1994, 1995) reported 1.82 and 2.69, 1.33 and 2.77, 1.69

and 2.76, and 1.45 and 2.2 in worker and drone cells, respectively.

Model Simulation for fertility. The model can be used to simulate the impact of different fertility rates on the total mite population obtained from worker and drone cells. This particular simulation is done utilizing worker cells. The fertility rates chosen for this simulation were taken from the literature. They include 70, 80, 85 and 95% fertility rates. In the first year of infestation, mite populations reached 277, 803, 2154 and 3359 for the above fertility rates, respectively (Figure 24). This clearly illustrates the important role that fertility rate plays in the overall population dynamics of the mite.

These various fertility rates corresponded to differences in the rate of colony collapse (Figure 25). Fertility rates of 80% and above caused colony collapse within two years, with the earliest collapse associated with the highest fertility rate. A fertility rate of 70% caused the population to peak in August of the third year, with colony collapse in the spring of the fourth year.

Model Simulation for fecundity. The model was used to simulate the impact of number of offspring on mite population dynamic. Figure 26 illustrates the impact of small changes in the average number of offspring produced on the overall mite population dynamics. It can be seen, that even small changes in average number of offspring, can have a huge impact on the mite population, with great repercussions on the health of the bee colony. For example, change from 1.5 to 1.6 offspring can cause the mite peak population to increase from 6,000 to 10,000 mites in one year period.

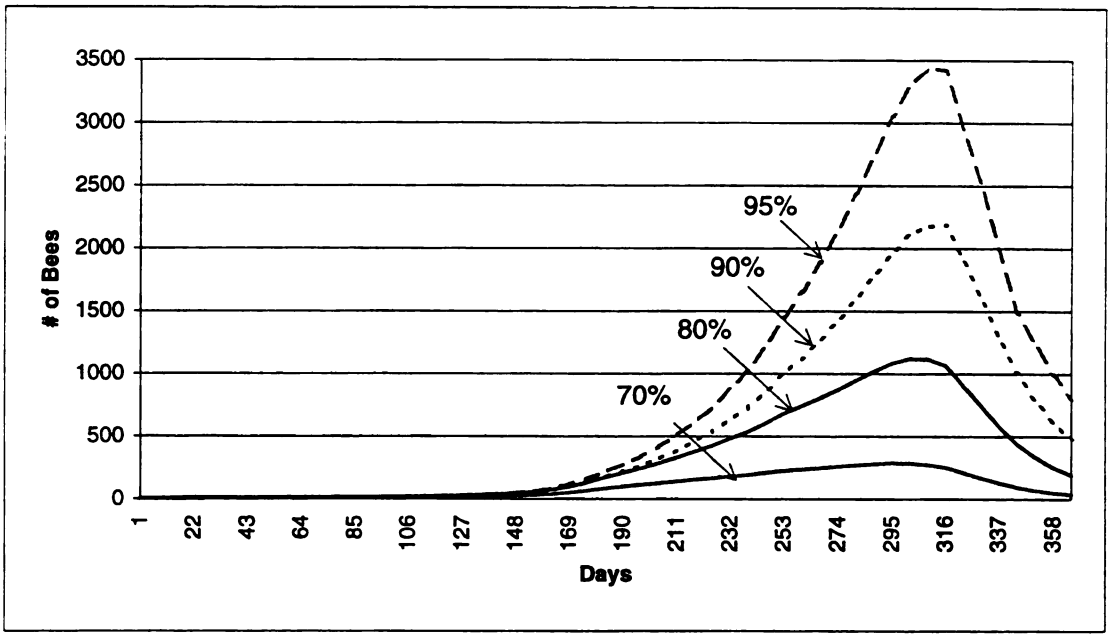


Figure 24. Mite populations when female mites have different fertility rates in worker cells

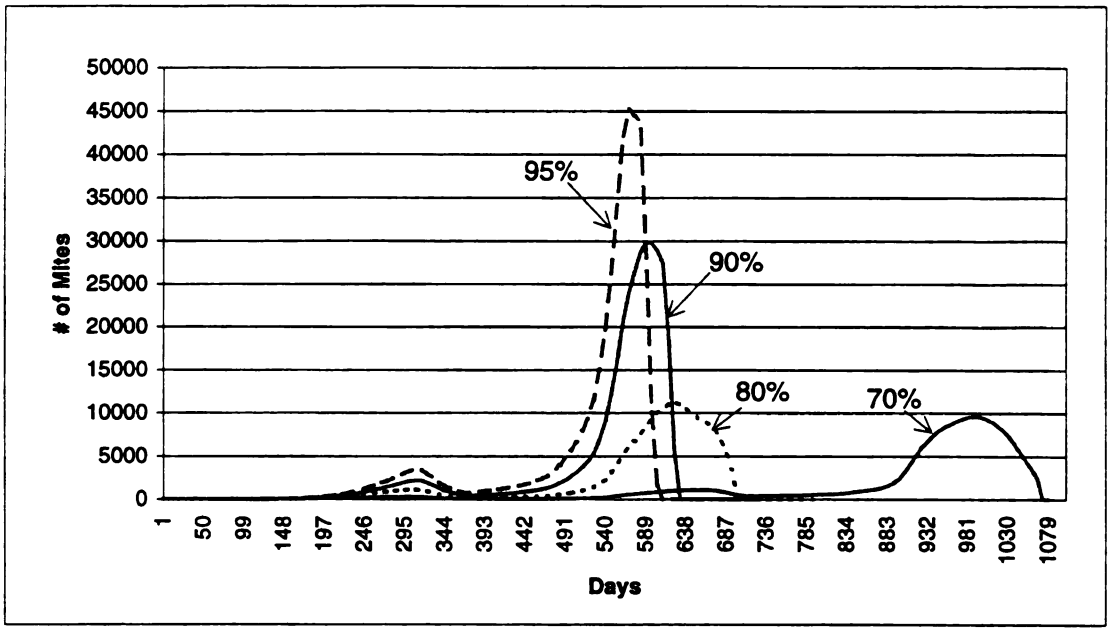


Figure 25.Mite population development until the colony collapse when Varroa females have different fertility rates.

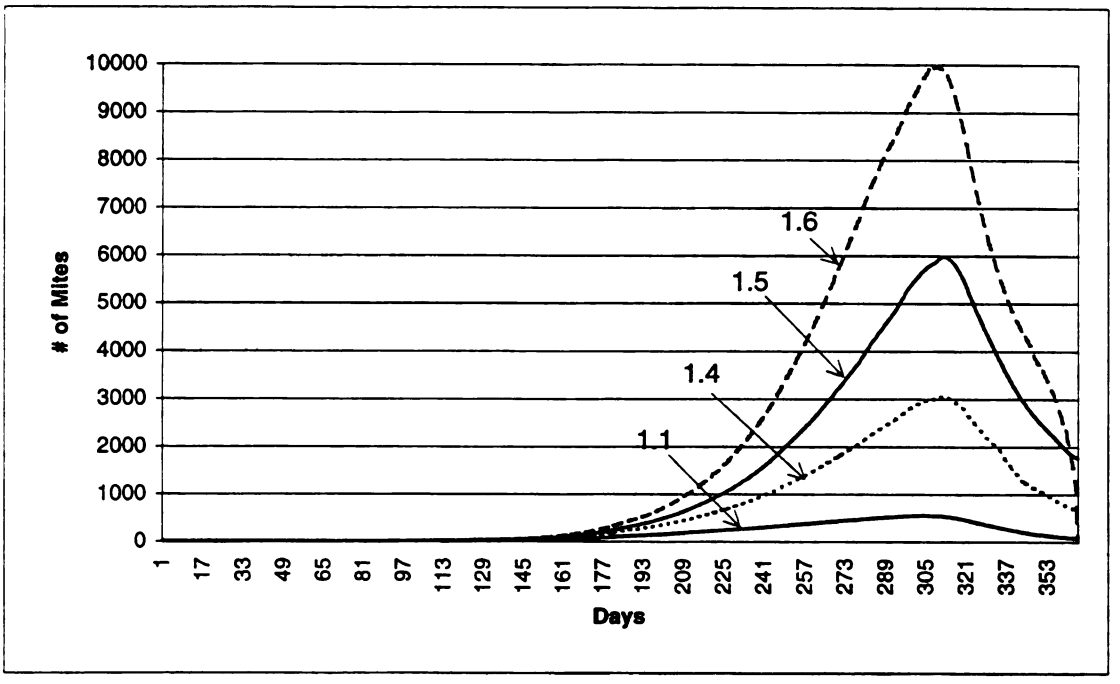


Figure 26. Mite population development in one year with different average number of offspring.

Post-capping period

Literature review. The length of the bee brood post-capping period will effect the number of offspring produced by *Varroa jacobsoni* and it is one of the traits that is considered when attempting to find a stock of honeybees tolerant or resistant to Varroa. Post-capping period has been studied in different races of *Apis mellifera*.

The sealed brood stage of *A. cerana* lasted 10.9 days. The whole development is 18.5 days for the worker (Dung *et al.*, 1993); and 22.8 days for the drone (Tan *et al.*, 1993). Dung *et al.* (1993) observed that *A. mellifera* has slightly longer developmental times of 19.4 and 24 days, respectively, in their research in the same region.

Mortis and Hanel (1984) and Mortis (1995) showed that the postcapping period of the workers of *A. m. carnica* ranged between 11.7 and 12.5 days. Subousbo (1986) measured maximum differences of up to 1.15 days for the duration of the capped stage of worker brood in *A. m. ligustica* colonies. Buchler and Drescher (1990) observed differences in the length of the capped stage of up to 9h between different strains (*A.m. carnica*, *A.m. mellifera* and Buckfast) and up to 19 h within individual colonies.

Africanized bees in South America have an 11 day average post-capping period for worker and pupae. This allows only one or two female offspring of Varroa per female mites (Camazine, 1988); whereas, mites on European honey bees, with a mean post-capping period of 12 days, can each produce up to three offspring (Rehm and Ritter,1989; Schulz, 1984). The mite caused little damage to *A. m. capensis* (cape bee) because the brood stage of this species lasts 9 days, approximately two days shorter than *A.m. carnica* (Hanel, 1984). In this sub species the mite reproduction is restricted in worker brood. Only 21% of the mites can

produce even 1 fertile offspring, and the other 79% are unlikely to produce any viable offspring (Moritz and Mautz, 1990).

The post-capping period of the drone is approximately the same for European and Africanized bees, approximately 14 days (Berthof, Jay 1963,Wiese 1972). Selection for a shorter post-capping stage may be a possible way to achieve resistance, particularly in the light of its high heritability (Moritz, 1985).

Buchler and Drescher (1990) determined the correlation of both strain and season: for 21 colonies, checked twice, a positive correlation between the length of the capped stage and the infestation level was estimated (=0.48) indicating that, on average, a reduction of the length of capped stage by one hour led to an 8.7% reduction in the final mite population level.

Model Simulation. The next simulation focused on the effect of changing postcapping periods. The data used in this simulation is roughly adapted from Martin (1977) as described in the above introduction. Differences in postcapping can have a major impact on mite population dynamics in the first year of infestation (Figure 27); as well as throughout the life of the colony (Figure 28). As the post-capping period increases, the number of offspring increase, and the colony collapses at a faster rate. If the post-capping period can be reduced to ten days, then the mite impact on the bee population will be minimal (Figure 29).

Reproductive cycle

Literature review. Ruijter (1987) artificially transferred mites from cell to cell and found that the mother mite is able to reproduce as many as seven times. Schulz (1984) reported that 78% of the mites reproduce only once and 22% reproduce twice. Mikityuk *et al.* (1976) observed an additional reproduction cycle, he stated that 78% of Varroa produce

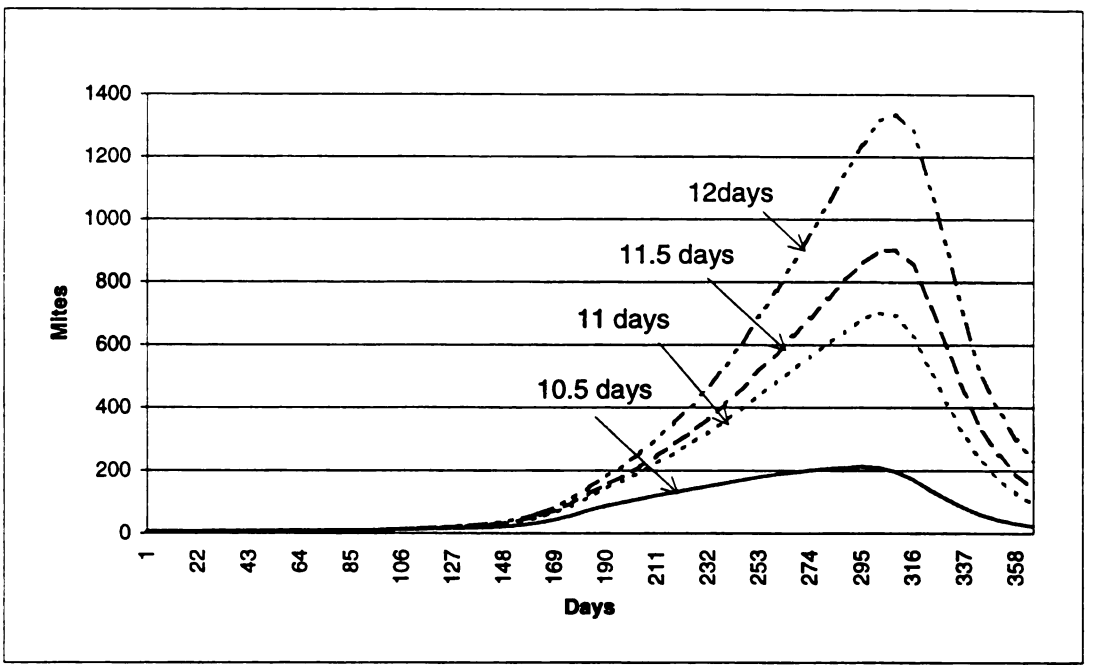


Figure 27. Mite population development in the first year when worker brood have different post-capping periods.

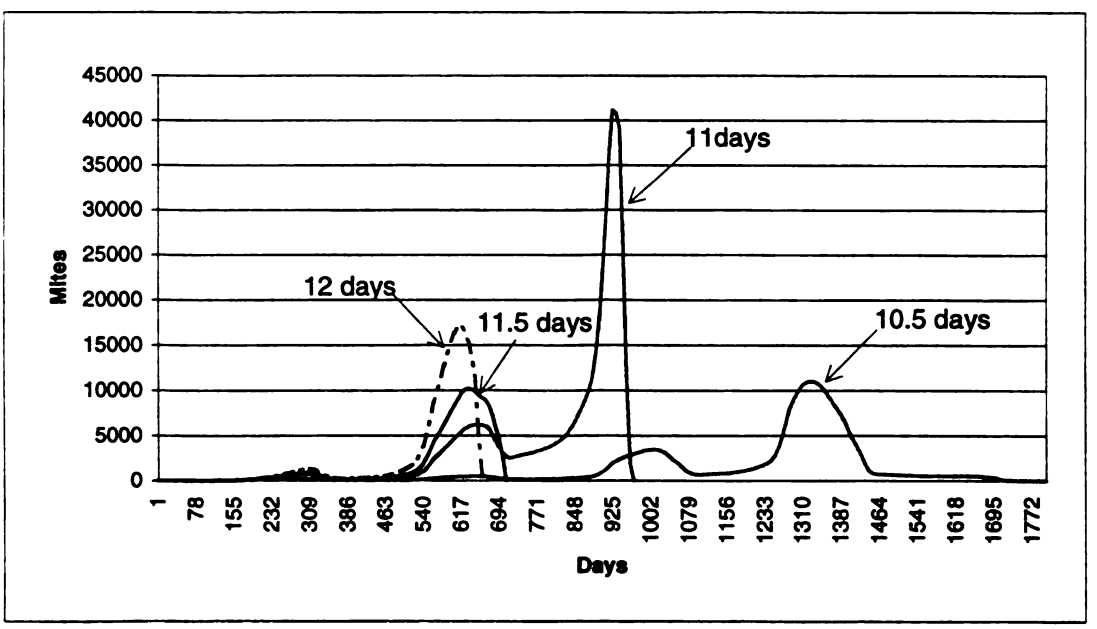


Figure 28. Mite population development until the colony collapse when worker brood have different postcapping periods.

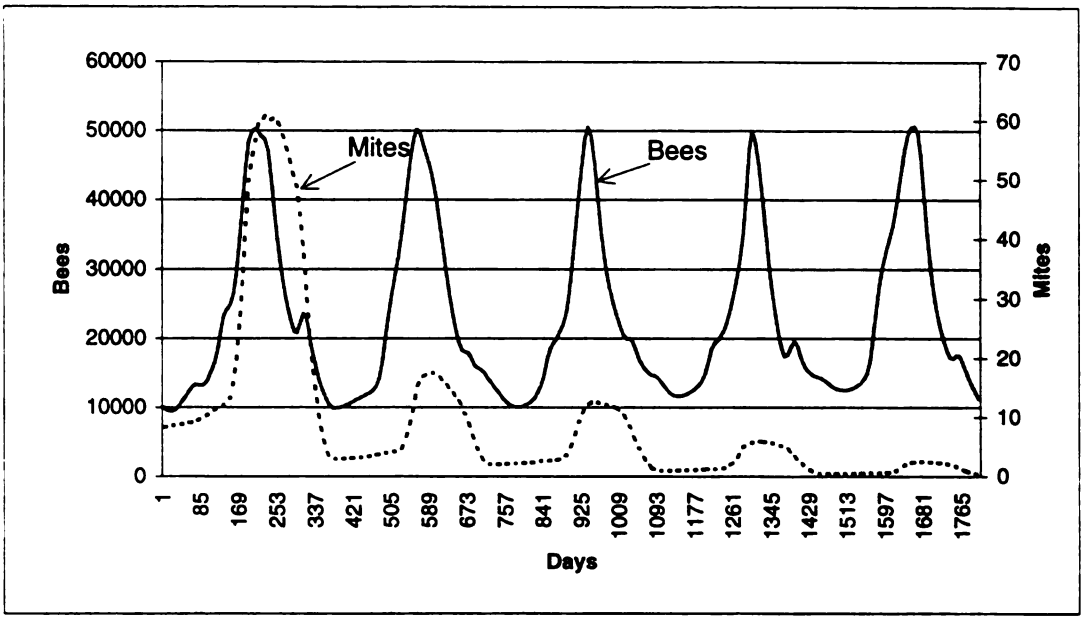


Figure 29. Mite and bee populations development when worker brood have 10 day post-capping period.

only once, 18% produce twice and 4% produce three times for an overall mean number of 1.26 reproductive cycle per female mite. Mikityuk (1979) and Grobove (1977) stated that 1.9% and 4% of the mite reproduce four times respectively. Fries and Rosenkranz (1993) reported that 13% of the mites reproduce three times, their sample was 475 mother mites. Wended and Rosenkranz (1993) found that 4.1% of the mites produce three times with an overall mean of 0.88 reproductive cycle per mother mites. Recently, Fries and Rosenkranz (1996) using full-size colonies reported that under optimal conditions the mean number of reproductive cycles by Varroa is greater than 1.5 but less than 2.

Model Simulation. The importance of the reproductive cycle can also be easily simulated (Figure 30). The parameters chosen for the simulation were suggested by Fries (1994, 1996) and Engles (1994). The mite population will almost double if the reproductive cycle is increased by 0.2.

Phoretic periods

Literature review. After emergence from the brood cells, the female mites reside a certain period on adult bees in the colony before they invade new brood cells (Boot *et al.*, 1993; Boot *et al.*, 1994). Boot *et al.*, (1996) stated that the length of this period strongly affects the population dynamics of the mites, because mites cannot reproduce while they reside on adult bees and therefore reproduction is delayed. In addition, the period on adult bees may affect the population dynamics of the mites since some of the mites will die during their stay on adult bees and also it might reduce the number of offspring per mother mite (Beetsma and Zonneveld, 1992). Thus fitness of mites increases by minimizing their stay on adult bees (Boot and Calis, 1993). Schulz (1984) reported after a phase of 1-20 days (44%

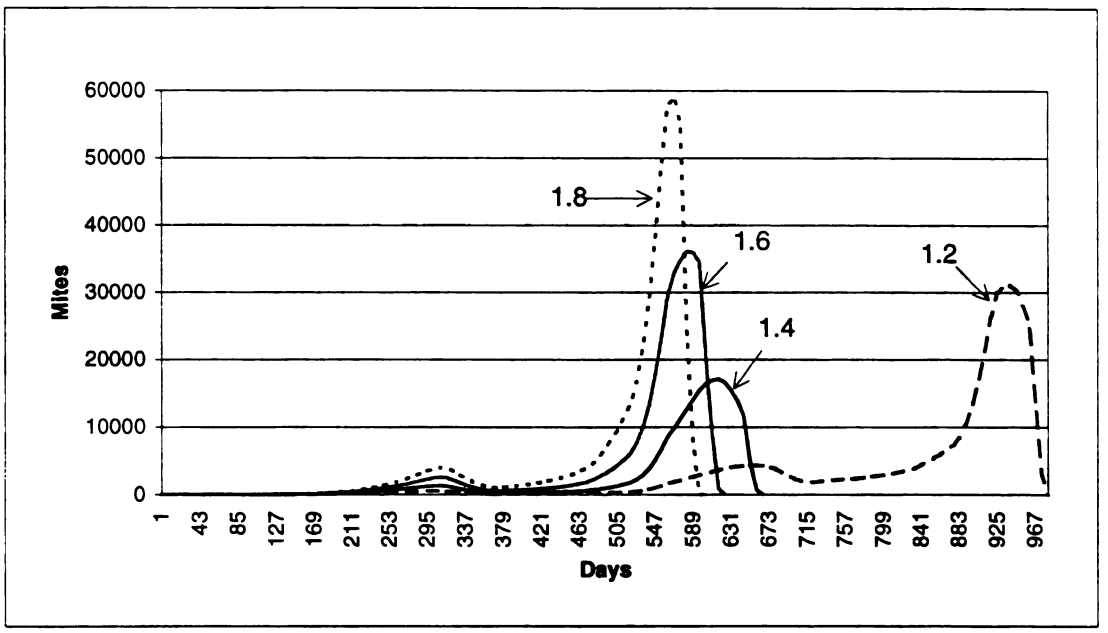


Figure 30. Mite population development when female mites have different reproductive cycles.

within 6 days) on adult honeybees, the female mite enters the brood cell for reproduction. He found that the phoretic period was 4.5 days for old mites, 10.7 days for young mites and 7.4 days for a mixed population of mites. (Boot *et al.*, 1993; Boot et al., 1994) stated that during the brood rearing the mean residence time of mites on adult bees is maximally 1-3 weeks, depending on the number of brood cells available for mite invasion. Woyke (1987) reported that mites have an average phoretic period of 4.7 days in a mixed population and 5.9 days for young mites. Grobov (1977) reported a range of 4-13 days.

Mites begin to invade brood cells during limited periods preceding cell capping with a fairly constant rate until cells are capped, about 50 and 20 hours for drone and worker respectively (Ifantidis, 1988; and Boot *et al.* 1992).

Model Simulation. The effect of different phoretic periods can also be illustrated with this model (Figures 31, 32). The phoretic periods chosen were 4.9, 6.9, 8.9, and 10.9 days. These correspond to a maximum population of 1883, 991, 577, and 376 in the first year of infestation, respectively. The longer the phoretic period, the less of a population increase (Figure 31). Running the simulation over a number of years, it was found that colonies with an average phoretic period of 4.9 and 6.9 days collapsed in the second year, while those with longer periods (8.9 and 10.9 days) did not collapse until the third year (Figure 32).

DISCUSSION

The model is used to evaluate some of important traits involved in resistance or tolerance of honey bees against Varroa colonies such as grooming, brood removal, brood

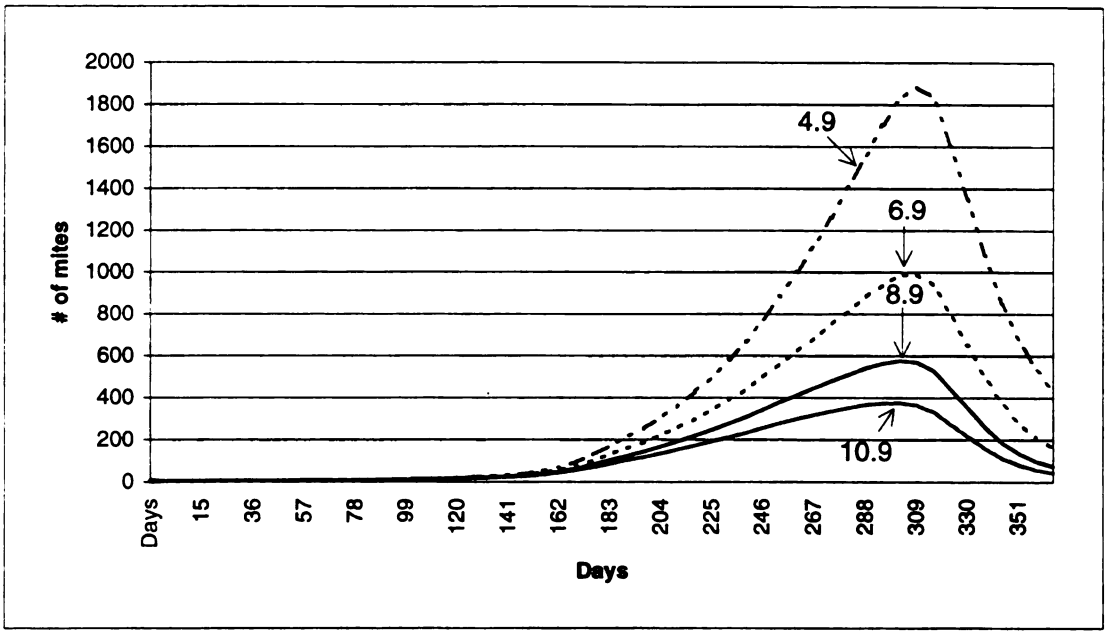


Figure 31. Mite population development in the first year when female mites have different phoretic periods.

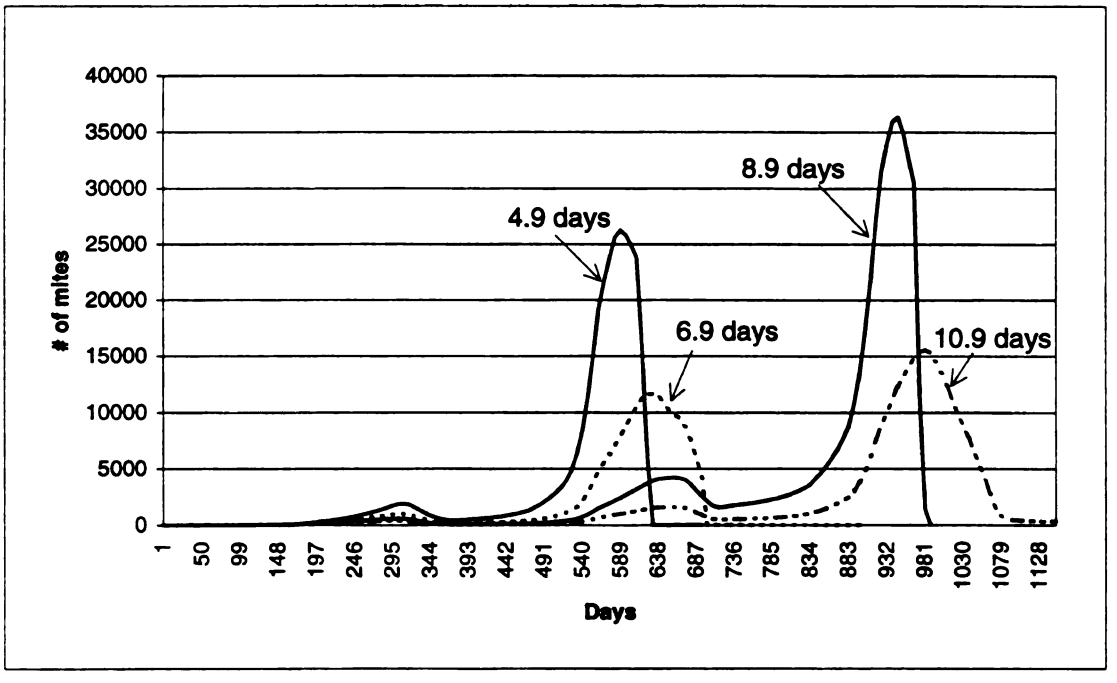


Figure 32. Mite populations development until the colony collapse when female mites have different phoretic periods.

attractiveness, infertility of mites, and post-capping period, and reproductive cycle. The results obtained indicate that the model is a valuable tool for predicting the changes in mite and bee populations resulting from varying a single factor concerning the above mentioned traits. The values were obtained from research literature when available.

For long term solutions to the Varroa problem, priority should be given to research on genetic improvement of colony defense mechanisms (Buchler, 1994). Since selection program for such mechanisms will take a very long time, it is important to concentrate on the most effective resistant trait that effects the mite population. The results from the model simulations illustrate the effect of these traits on the bee and mite populations and it showed that any thing that effected mite reproduction such as number of offspring, fertility, reproductive cycle and phoretic period are the most important traits on which to concentrate.

Treatment efficiency and time of treatment were also simulated in this model and the results show that one treatment is sufficient to control the mites for two years at least if there is no reinvasion from outside and if the beekeepers follow the label concerning length of treatment. However, reinvasion is inevitable in the field and that explains the failure of the control measure and colony death even when treated once a year. This shows how important it is for beekeepers to try to reduce reinvasion by cooperating with each other in the same area, by treating in the same season, and by including in their management practices help in reducing drifting, robbing, swarming, etc.

Controlling the mites by means of non chemical measures is labor intensive, time consuming and is not practical for large operation beekeepers. Although, intensive drone removal reduce high portions of the mite population, still it is not successful in controlling the mite the second year when the population becomes high.

Trapping comb and hyperthermia techniques alone will not work for more that two years in high or moderately high population colonies as the simulations indicate and these results are in agreement with Maul (1988) who reported that the technique is good for two or three years, but reported that mite population levels continue to increase after that time frame. Fries *et al.* (1993) stated that the trapping comb technique might be insufficient for controlling mites in all colonies over a period of several years due to the high mortality during the third and fourth experimental year.

The conclusion is that one biological control technique alone would not be sufficient to control the mite but when selecting for bees that have some traits that reduce mite populations, naturally biological control might work.

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DISCUSSION

Deflinado-Baker and Houck (1989) suggested a lower virulence of mites from North America compared to mites from Europe on the basis of the hypothesis of the South America origin of the mite in the US. Our results agree with other research from the US (Page and Kraus, 1995; Delaplane and Hood, in press 1997) and disagree with Deflinado-Baker and Houck. In Georgia, Delplane and Hood (1997, in press) started with new packages of bees which contained a small incipient population of *V. Jacobsoni.* The mite population increased in June to 427±110, in August to 3172±324 and to 6662±2127 in October. Kraus and Page (1995) reported that in the Mediterranean climate of California the initial population is capable of increasing 300-fold during one year, they started with 50 mites at the end April and the mite population increased to 2,367 in October. When the researchers started with 50 mites at the end of October, the mite population increased to 1,620 in April. Our results show that over the period of one summer, the mite population increased 81, 188 and 193-fold for the groups that were infected with 5, 10 and 25 mites respectively, when using the sticky board method of estimating mite population. This was an average of 154-fold increase. When estimating the population from the live bee method, there was a 352, 225, and 125-fold increase, respectively. This method had an average increase of 234-fold.

When comparing the mite population in US with that in Europe, the increase averages about 10-fold per year (Ritter, 1984; Fries, 1991; Korpela *et al.*, 1992); but can increase up to 100-fold within one summer (Fries *et al.*, 1991).

Comparing reproduction rates obtained in this study with other studies, it is found that the mite reproduction rate of 86.8% in worker and 93% for drone broods was very representative of what other researchers found. Blum (1989) reported mite reproduction rates at 88.7%, Fuchs and Langenbauch (1989) recorded 92.7% and Buchler (1990) found 86.6% in worker brood cells. In drone cells, Fuchs and Langenbach (1989) also recorded 92.2% fertility rates in drone cells.

The percent of mites that did not reproduce (11.0% in workers and 7.1% in drones) also was similar to figures presented by other researchers. In worker cells, Sulimanovic *et al.* (1982), Schultz (1984), Moosbeckhofer *et al.* (1988), Fuchs and Langenbach (1989), Ifantidis (1990) and Boot *et al.* (1995) reported infertility rates in worker cells of 13, 16, 7, 7, 14.1, and 8-12%, respectively. Fuchs and Langenbach (1989), Ifantidis (1984), and Schultz (1984) found lower levels of infertility in drone cells also. They reported 8, 4, and 5%, respectively.

Some of the mother mites produced only male offspring. This is probably because they had not mated, since haploid eggs of Varroa mites develop into males (de Ruijter and Pappas, 1983). Martin (1995) attributes this partly to the death of the male before he is able to fertilize his sisters. He found in earlier studies, that 20% of the males died before they mated in worker brood (1994) and 10% in drone cells (1995).

In this study, it was found that 5.1% of the offspring were male only in worker cells.

This was similar to other studies. Boot *et al.* (1995), Schultz (1994), Moosbeckhofer *et al.* (1988) and Fuchs and Langebach (1989) reported a rate of 8-10, 6, 3 and 3%, respectively. For drone cells, a rate of 3% was observed. Fuchs and Langebach (1989) reported a rate of 1%.

The other parameter that was measured was the percent of mother mites that died in brood cells. It was found that 2.3% died in worker cells and 2.7% in drone cells . Only one other researcher reported this statistic (Martin, 1994). He found a higher percentage in drones (7.7%), and a similar rate in workers (2%). He found that 32% of the deaths in drone cells were caused by failure of the mite to emerge from the brood food and found they were trapped in the cell wall. The percentage rose to 50% in worker cells.

The model simulates bee and mite populations and illustrates the effect of the bees on the mite population and the effect of the mites on the bee population. When starting with different initial infestation, 5, 10 or 20 mites, the population peaked at 690, 1,339 and 2,521 in the first year, and as the initial infestation increased, the population peaks early in the season in the second year. The same trend will continue the next year until the damage threshold is reached. It seems that the threshold depends on the ratio of mites to bees. If the number of mites is high in proportion to bees, the bee population can not support the colony and it will die.

The model is used to evaluate some of the important traits involved in resistance or tolerance of honey bees against Varroa colonies such as, grooming, brood removal, brood attractiveness, infertility of mites, post-capping period, and reproductive cycle. The results obtained indicate that the model is a valuable tool for predicting the changes in mite and bee populations resulting from varying a single factor concerning the above mentioned traits. The

values used as a parameter in the model were obtained from research literature when available. The results from the model simulations illustrate the effect of these traits on the bee and mite populations and it showed that any thing that effects mite reproduction such as number of offspring, fertility, reproductive cycle and phoretic period are the most important trait for which to select.