

Modeling Of Honey Bee And Varroa Mite Population Dynamics

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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 were: initial mite population, number of female offspring per mother mite in both worker and drone brood, number of reproductive cycles, fertility, percent mite preference for drone versus worker brood, phoretic period, mortality, and removal of infested brood cells by hygienic worker bees. 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 infestation rates (5, 10 and 20 mites). The first year infestation rate resulted in different maximum mite populations levels, and the estimate was 690, 1,339 and 2,521 for the three rates, respectively. In the second year, the mite population maximum 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. The results from these model 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 scientists to vary and check the influence of single factors on the mite population development. In addition, it should help in the development of research hypotheses to test under field conditions. It also was the hope of this modeling project that by integrating past research results it would help identify research gaps that need further investigation in an effort to find better ways to control mite populations in bee colonies.

Key words: Honeybee, Varroa mite, Bee modeling, Varroa and honeybee Saudi Arabia, mite modeling.

Introduction

Modeling is a valuable tool that helps in the understanding of complex societies, such as honeybees, 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. Their 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 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 temperature 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 0-31 °C, 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.

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 195 (Fukuda & Sakagami, 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 honeybee 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 mite 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 *Varroa jacobsoni* does not normally reproduce when it infests worker brood of the Eastern honeybee, *A. cerana*. Extensive mite reproduction occurs only on drone brood. In *Apis mellifera*, a portion of the infesting Varroa mites does not reproduce. Blum (1989) reported mite reproduction rates at 88.7%, Fuchs and Langenbach (1989) recorded 92.7% and Buchler (1990) found 86.6% in worker brood cells. In worker cells, Sulimanovic *et al.*, (1982), Schutz (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 (1980) found lower levels of infertility in drone cells. They reported 8, 4, and 5%, respectively. Ritter and De Jong (1984) observed only 43 of mites in *A. m. ligustica* in the worker cells in South America to be fertile. Marcnageli *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 *Apis 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 *Apis mellifera 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) Infantidis (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 mite enters a brood cell to reproduce is a key factor in determining population growth of *Varroa 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 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 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 4.15 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 honeybees, 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.

Mite begin to invade brood cells during a limited period proceeding 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 *Apis cerana* F., the original host of *Varroa 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*. Bucher *et al.* (1992) also compared grooming in *Apis cerana* and *Apis mellifera* and found successful mite removal in 75% of the cases in *Apis cerana*. In *Apis mellifera*, 48% of the mites removed by grooming. Fries *et al.* (1996) reported lower numbers in full-sized colonies of *Apis cerana*, the bees removed 56% of 220 mites in 6 h. and, of those, 30% were damaged; results for *Apis mellifera* colonies were 21% of 280 mites were removed and 12% were damaged.

Ruttner and Hanel (1992) examined the natural mortality of five *Apis mellifera 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 *Apis mellifera* bees.

Rothenbuhler (1964) described hygienic behavior of bees 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 *Apis mellifera* against Varroa mites

was observed in both *Apis cerana* and *Apis mellifera*. Rath and Drescher (1990) showed that the *Apis cerana* workers were successful at detecting, uncapping and removing 985 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 *Apis mellifera 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 was 10.9% for their own brood and 15.4% for another colony's brood, when number of mites increased to two, removal rose to 32.2% and 41.9%, respectively. Boecking and Ritter (1993) reported workers in 15 test *Apis mellifera 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

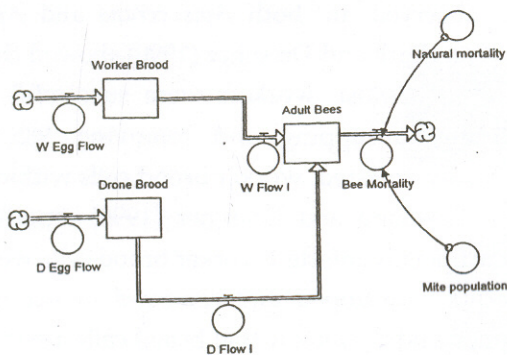


Fig 1. Honeybee components of the modeling projects.

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 honeybees, *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 1,800 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 assumption that the adult population must have at least 1,000 members to support the queen's egg laying (If Adult population > 1,000 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

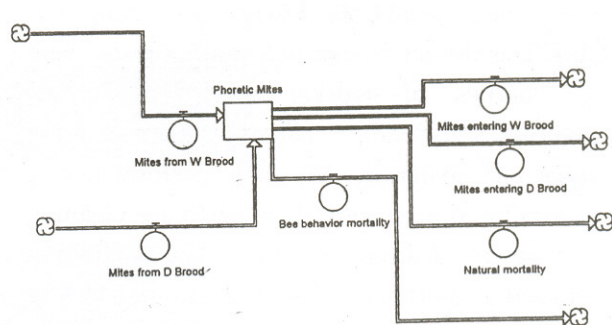


Fig 2. Mite components of modeling project.

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 ($p < 0.001$).

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

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

Table 1. Parameters used for model simulation of *Varroa jacobsoni* and honeybees *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 temperature on CD Rom)	***
Foraging	Percent foragers under Midwestern conditions (DeGrandi-Hoffman, 1989)	***
Adult	Coefficient of adult factor taken from Midwes research data (DeGrandi-Hoffmann, 1989)	***
Worker postcapping period	12 days	***
Drone postcapping period	14 days	***
Total worker brood	Conveyer stock, with 12 days 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 <i>et al.</i> , 1994; Boot <i>et al.</i> , 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		1.3 (Ifantidis, 1984)
Number of female offspring produced in a drone cell		2.7 (Schulz, 1984, Ifantidis, 1984)

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 develop 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:

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

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

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:

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

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

where:

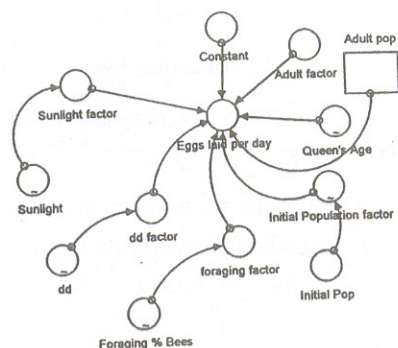


Fig 3. Honeybee egg laying components of the modeling projects.

dB_D = Change in drone brood

B_D = Drone brood

F_{DI} = Eggs becoming drone brood

F_{DII} = Flow from drone brood

Db_w = Changes 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 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:

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

where:

BP = Bee population

F_{WII} = Flow from worker brood

F_{DII} = Flow from drone brood

M_{BP} = Bee population Mortality

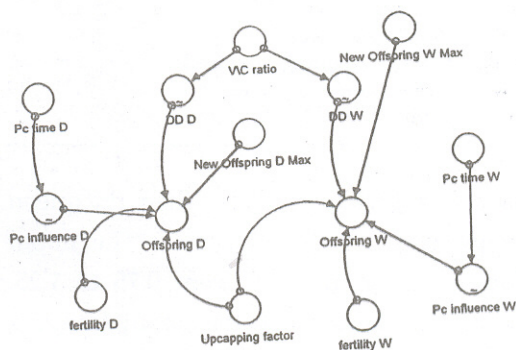


Fig 4. Mite population components of the modeling project.

Honeybee mortality came from either death due to natural causes or death due to varroaosis. Honeybees 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:

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

where:

M_{BP} = Mortality of bee population

BP = Bee population

MP_{DC} = Mite population entering drone cells

MP_{WC} = Mite population entering worker cells

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:

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

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

When mites are ready to reproduce offspring, they enter brood cells, with a preference for drone brood cells. The number that enters 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 fertility rate of the mite, the number of female 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:

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

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

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 = Fertility rate in drone cells

DD_D = Density dependence in drone cells

I_D = Post-capping influence in drone brood

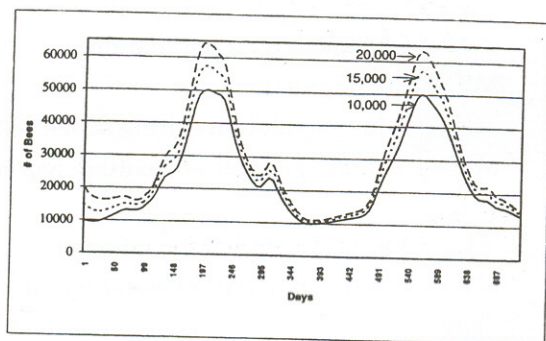


Fig 5. Adult bee population development when starting with different initial populations in January.

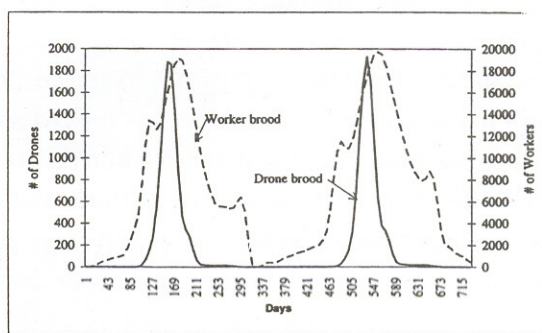


Fig 6. Worker and drone brood population development.

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 entering each cell. This is dependent on both the number of mites and the number of cells available. The total number of cells that are of the correct age to attract the mite determine the number of available cells. This part of age corresponds to the eight and ninth day after egg laying plus an additional two hours on the tenth day for drone brood, and to 20 hours of the eight day for worker brood. Delay functions were used to simulate this period of attraction. Total number of available drone brood cells 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, 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 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.

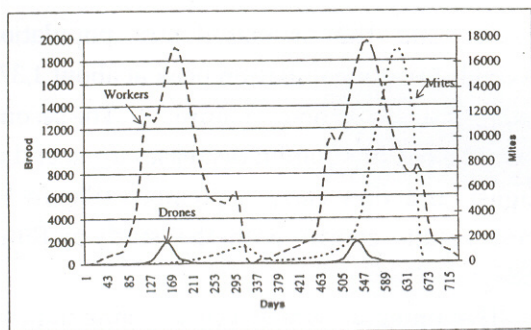


Fig 7. Mite population in correlation with worker and drone brood development.

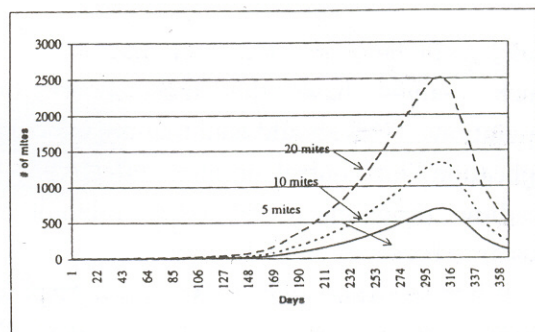


Fig 8. Mite population development in the first year when starting in April with different initial infestation.

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 honeybees, 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:

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

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

Results 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

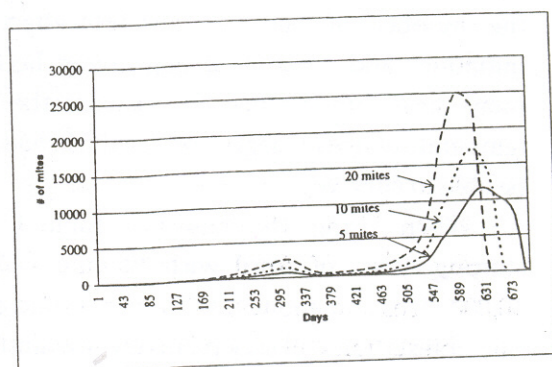


Fig 9. Composition between mite population development when starting with different initial infestations in April until the collapse of the colony the second year.

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 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 5,000 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 overwintered 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 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 mites, 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 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. Figure 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.

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بناء نموذج محاكاة لتطور حياة نحل العسل وحلم الفاروا

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المملكة العربية السعودية

الملخص: تم دراسة تطور حياة نحل العسل وحلم الفاروا وعلاقتها ببعض باستخدام نموذج محاكاة تجاري يسمى ستيل ٢. ستيل ٢ يوفر تقنية محاكاة مركزة غير رياضية تسمح للمستخدم بتكوين معادلات رياضية باستطاعتها دراسة تطور مجموعة سكانية خلال وقت محدد باستخدام أقل ما يمكن من المتغيرات. يقوم النموذج بتكوين إحصاء سكاني على فترات زمنية محددة وتكون المخرجات إما رسوم بيانية أو معادلات أو جداول أو رسوم توضيحية. المتغيرات التي استخدمت في نموذج الحلم كالتالي: عدد أفراد الحلم في بداية الإصابة، عدد المواليد الإناث لكل أم في العيون السداسية للشغالات والذكور، عدد المرات التي تلد فيها أنثى الحلم، خصوبة الأنثى، نسبة أفضلية الحلم لعيون الشغالات والذكور، الفترة التي يمضيها الحلم متعلق على جسم النحلة، نسبة الموت ونسبة تنظيف العيون السداسية من الحلم. العلاقة بين النحل والحلم أيضاً درست في النموذج، على سبيل المثال درس تأثير إصابات مختلفة في بداية الموسم على تطور واستمرارية طائفة النحل. فعند العدوى بخمسة أو عشر أو عشرين حلم في بداية الموسم كانت نسبة الإصابة مختلفة في السنة الأولى حيث سجلت أعداد الحلم كالتالي: ٦٩٠ و ١٣٣٩ و ٢٥٢١ عندما كانت أعداد الحلم على التوالي. وفي السنة الثانية وصلت أعداد الحلم لأعلى نسبة وهي ١١٠٠٠ و ١٧٠٠٠ و ٢٥٠٠٠ على التوالي. على العموم كان موت الطوائف مرتبط بكمية العدوى في بداية الموسم حيث فقدت الخلايا التي كانت معدية بعشرين حلم أولاً تلاها الخلايا المعده بعشرة حلم وأخيراً الخلايا التي معده بخمسة حلم. أيضاً ممكن تغيير بعض المتغيرات في النموذج مثل طول فترة الحضنة، والخصوبة، ونسبة المواليد، كما يمكن أيضاً إدخال طرق مكافحة كيميائية وبيولوجية. هذا النموذج يمكن المتخصص سواء كان نحال أو باحث من تغيير طرق المكافحة ومواعيد استخدامها ليحصل على أفضل نسبة فعالية للطريقة المستخدمة. الهدف من بناء هذا النموذج هو تطوير أداة لتوقع كثافة النحل والحلم تحت ظروف معينة والسماح للمختصين بدراسة تأثير أحد المتغيرات أو بعضها على تطور نمو الحلم. كما سيساعد هذا النموذج على تكوين وتطوير فرضيات لتختبر وتطبق في الحقل. كان الأمل أيضاً من بناء هذا النموذج استخدام نتائج الأبحاث المتوفرة في هذا المجال ودمجها مع بعض والكشف عن بيانات الأبحاث الناقصة ليتم التركيز عليها مستقبلاً لنصل إلى أفضل الطرق لمكافحة الحلم في طوائف نحل العسل.