A MATHEMATICAL MODEL OF *VARROA* MITE (*VARROA DESTRUCTOR* ANDERSON AND TRUEMAN) AND HONEYBEE (*APIS MELLIFERA* L.) POPULATION DYNAMICS

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ABSTRACT - A mathematical model of population interactions between *Varroa destructor* and a honeybee colony is described. Validation tests indicate that the model generates mite population predictions that are similar to those from actual colonies including: weekly mite-drop, daily rates of population increase, and exponential growth rates for mite populations. The model predicts that colony survival thresholds for mite populations and the effectiveness of miticides such as fluvalinate are dependent on climate and the yearly brood rearing cycle in a colony. Miticides applied in the late summer provide the best chances for the survival of heavily infested colonies. The model also predicts that large mite populations treated with miticides in the spring will recover by autumn to levels similar to those in untreated colonies. This is because in the treated colonies the surviving mites infest drone brood at lower numbers per cell and this increases reproductive success and hence the growth rate of the mite population.
Keywords - *Apis mellifera, Varroa destructor* Anderson and Trueman, honeybee, population dynamics model.

INTRODUCTION

Varroa destructor Anderson and Trueman is an external parasite of honeybees (*Apis mellifera*) that can have devastating effects on colony population growth and survival. Foundress females invade brood comb cells just before they are sealed for pupation and parasitize the worker or drone (male) honeybee larvae inside. The foundress feeds on the pupating bee, and this initiates egg development and reproduction. The first egg laid by the foundress develops into a male, followed by eggs that develop into females. The female offspring mate under the sealed cell with either their brothers or with male offspring of another foundress, in the case of multiple infestations in cells. The mated females leave the cell when the bee emerges and in this phoretic stage search for new cells to infest (Sammataro *et al.*, 2000).

Many factors influence the growth rate of mite populations in colonies. Some of the factors pertain to the mite, while others are related to the biology, genetics and state of the colony population and to environmental factors that drive colony population growth. For example, mite population growth is influenced by the reproductive rate of foundress mites, especially when cells are single-infested or drone brood is available. Mite populations increase throughout the spring and summer as the colony population grows. In the autumn though, brood rearing declines and the number of multiple-infested cells increases. Multiple infestations cause a decline in both mite reproductive rates (Fuchs and Langenbach, 1989; Donzé *et al.*, 1996) and the longevity of workers that emerge from the cells (Kovac and Crailsheim, 1988).

Because the population dynamics of mites and honeybee colonies are so interwoven, it is extremely difficult to quantify the impact of any single factor alone on mite population growth or colony survival. For this reason, we constructed a mathematical model that combines weather conditions with honeybee and mite biology to predict the influence of *Varroa* on honeybee colony population growth and survival. In addition, the model simulates the effects of commercially available miticides and population increases from the immigration of mites into colonies (Kraus and Page, 1995).

The purpose of this paper is to describe the model structure, how parameter values were estimated and to compare model predictions with field data and observations. We also used the model to evaluate the influence of weather conditions in different geographic locations and the timing of miticide applications on mite population growth and colony survival.

Table 1. Equations used in the mite population dynamics model.

Parameter	Equation	Reference
BEE MODEL		
Eggs laid per day	D x L1 x N x P	1
D[a]	- 0.0006 x Degree days^2 + 0.05 * Degree days + 0.021	1
L1	- 0.0262 x Daylight hours^2 + .809x Daylight hours - 5.15	1
N	Log_{10} [(Number of foragers x 0.001) +1]x 0.672	1
P	Max eggs – 0.0027 x Lay days^2 + 0.395 x Lay days	1
Lay Days	Number of days queen has been laying eggs	1
Proportion drone eggs	S + (L2 x F)	1
S	1 – (-6.355 x Prop sperm^3) + 7.657 x (Prop sperm$^{2)}$ – (2.3 x Prop sperm + 1.002)	1
Proportion of maximum sperm number in spermatheca (PropSperm)	(5.5 x 10^6 – Current sperm) / 5.5 x 10^6	1
L2	Log_{10}(daylight hours * 0.1) * 0.284	1
F	Log_{10}(Num. foragers* 0.0006) * 0.797	1
Number of drone eggs	(Eggs laid per day * Proportion drone eggs) * 0.85	1
Number of worker eggs	(Eggs laid per day – Number of drone eggs) * 0.85	1
Egg development	3 days	2
Drone larvae development	7 days	2
Worker larvae development	5 days	2
Capped stage -drone	14 days	2
Capped stage -worker	13 days	2
Adult drone lifespan	21 days	IC[b]
Adult worker lifespan	21 days + Forager lifespan	IC
Forager lifespan	4 days to 16 days	IC
MITE MODEL		
Mites available to infest	[1 – exp(- (rD + rW))] * Number phoretic mites	3
rD	6.49 * Number of drone brood/B	3
rW	0.56 * Number of worker brood/B	3
B	Number of adult bees * 0.125	3
Mite reproductive rate	Defined by initial conditions if mites/cell <= 1.0, if cells are multiply-infested use the following equations:	
- In drone cells	-0.3(mites/cell)^2 + 0.151 * (mites/cell) + 1.11; r^2 = 0.65, F = 6.5, p = 0.05	4
- In worker cells	-0.233(mites/cell)^2 + 1.15*(mites/cell); r^2 = 0.81, F = 66.5, p = 0.01	4
Mites emerging from brood	Emerging foundress mites + Emerging mated female offspring	
Emerging foundress mites	Infesting mites * Survival rate * Prop first time * 0.60	5
Emerging offspring	Infesting mites * Survival rate * Mite reproduction rate	
Mites immigrating per day	Total immigrating mites * Daily proportion	IC
Daily proportion	F(X) x delta X	
- delta X	1/(Number of immigration days)	
- X	Proportion of immigration days completed + delta X / 2	
F(X) (Cosine)	1.188395*Cos(X)	
F(X) (Sin)	1.57078*Sin(PI*X)	
F(X) (Tangent)	2.648784*Tan(1.5*X)	
F(X) (Exponential)	(1.0/(e-2))*(exp(1-X) -1.0)	
F(X) (Logarithmic)	-1.0*log_{10}(X)	
F(X) (Polynomial)	-1.5*X^2 +3.0*X	

[a] Degree days are expressed as ambient temperature at time (t) – 0°C
[b] IC represents a value that is entered as an initial conditions at the start of a simulation
1 = DeGrandi-Hoffman *et al.* (1989); 2 = Jay (1963); 3 = Calis *et al.* (1999), 4 = Donzé *et al.* (1996), 5 = Martin and Kemp (1997).

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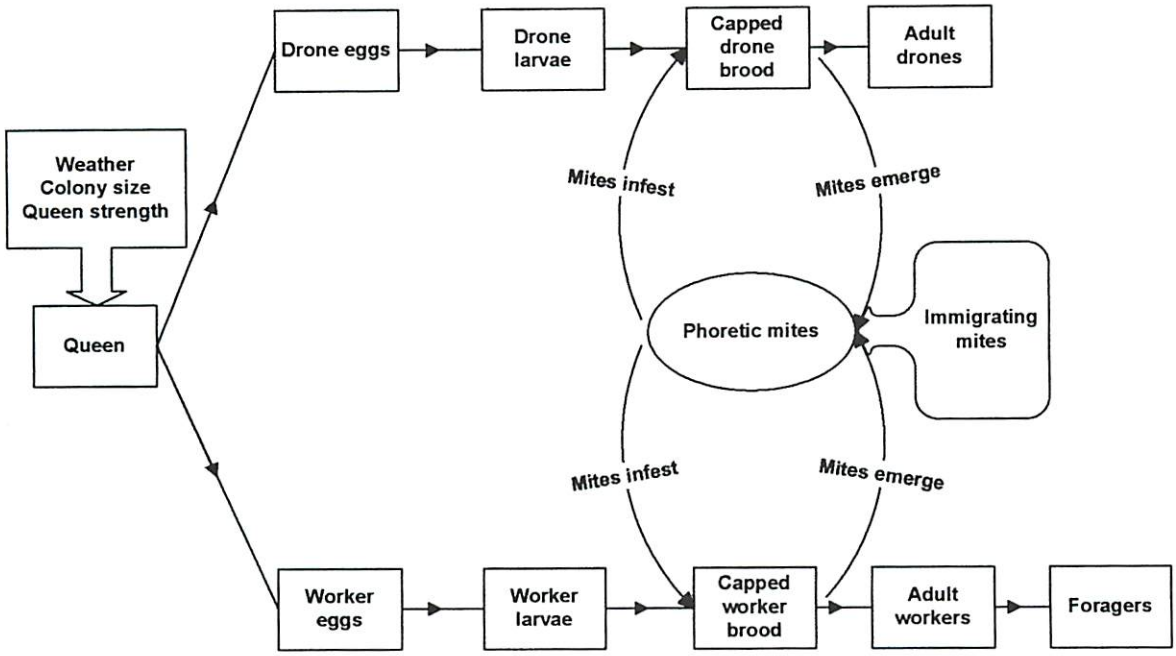


Fig. 1. Conceptual framework for honeybee colony and *Varroa destructor* population dynamics model

MATERIALS AND METHODS

Description of the model

Honeybee colony population growth - The model is written in Microsoft C++ and runs on the WINDOWS operating system. Copies of the program are available at http://gears.tucson.ars.ag.gov. The model simulates honeybee colony population growth using a time step of one day. The model structure (Fig. 1) and equations (Table 1) are based on the BEEPOP honeybee colony population dynamics model (DeGrandi-Hoffman *et al.*, 1989). The initial population of fertilized (worker) and unfertilized (drone) eggs, worker and drone larvae and pupae, and adult bees are entered at the start of the simulation. The adult bee population is comprised of house bees that are less than 21 days old, worker bees, foragers (workers older than 21 days) and drones. Colony parameters such as queen fecundity (i.e., the maximum number of eggs a queen can lay per day and the amount of sperm in her spermatheca), and the number of days a forager will live also are specified at the start of a simulation. The model then estimates the number of eggs a queen lays per day as a function of weather and colony conditions. The proportion of fertilized (worker) and unfertilized (drone) eggs produced each day is determined by colony population size, photoperiod, and queen fecundity (DeGrandi-Hoffman *et al.*, 1989). As queens age, sperm amounts become depleted and she lays higher proportions of unfertilized eggs. Eggs become larvae in 3 days, and cells are sealed 5 days later for worker brood and 7 days later for drones. Thirteen days after the cell is sealed, an adult worker emerges. Adult drones emerge 14 days after the cell is sealed. A new queen can be added to the colony at any time. This feature was added so that in simulations with time periods of a year or more there is the option of whether to include the effects of queens having a reduced capacity to lay fertilized eggs and producing more drones. The number of days before the new queen begins to lay and her fecundity also can be specified.

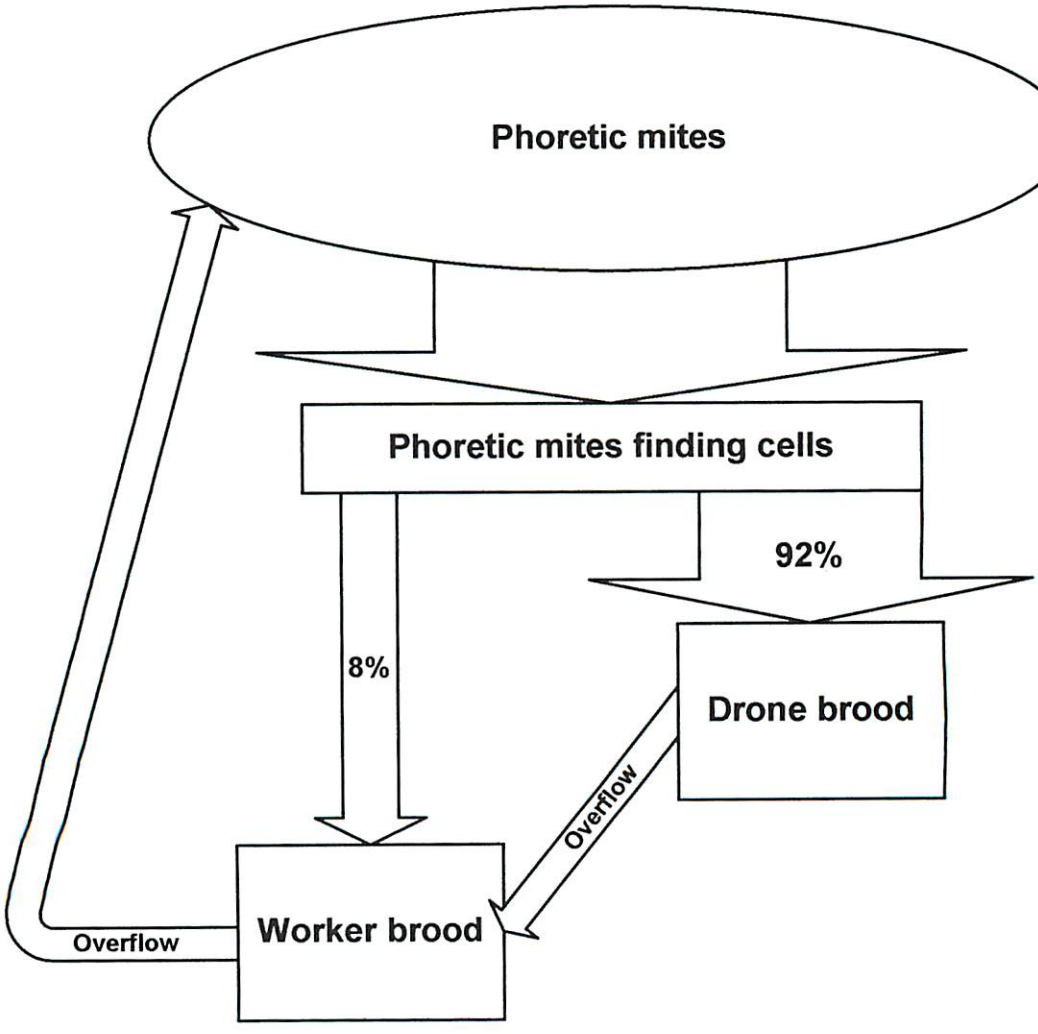
The model is initialized by evenly distributing the number of eggs, larvae, brood and adults specified by the user across each age group and lifestage. For example, if the colony population begins with 30 eggs, 10 eggs each will be initialized as 1, 2 or 3 days old. Adult worker bees live for 21 days as house bees, and then become foragers. The number of days that worker bees can forage before dying is initialized at the beginning of a simulation. If a worker bee emerges from a brood cell that has been infested with more than one foundress mite, its lifespan will be reduced (Table 2).

Mite reproduction - At the beginning of a simulation, values are entered for the initial number of mated female mites and their distribution in sealed worker and drone cells and on adult bees. Mites are evenly distributed across all age ranges of sealed cells and adult bees. Mites on the adult bees can infest available brood cells and reproduce.

Table 2. The percentage lifespan reduction of adult worker honeybees if infested with *Varroa destructor* during development.

Foundress mites per cell	Percentage lifespan reduction[a]
1	2
2	10
3	20
4	40
5	80
6	90
7	90

[a]Estimates of lifespan reduction percentages are based upon data in DeJong and DeJong (1983) and Kovac and Crailsheim (1988)



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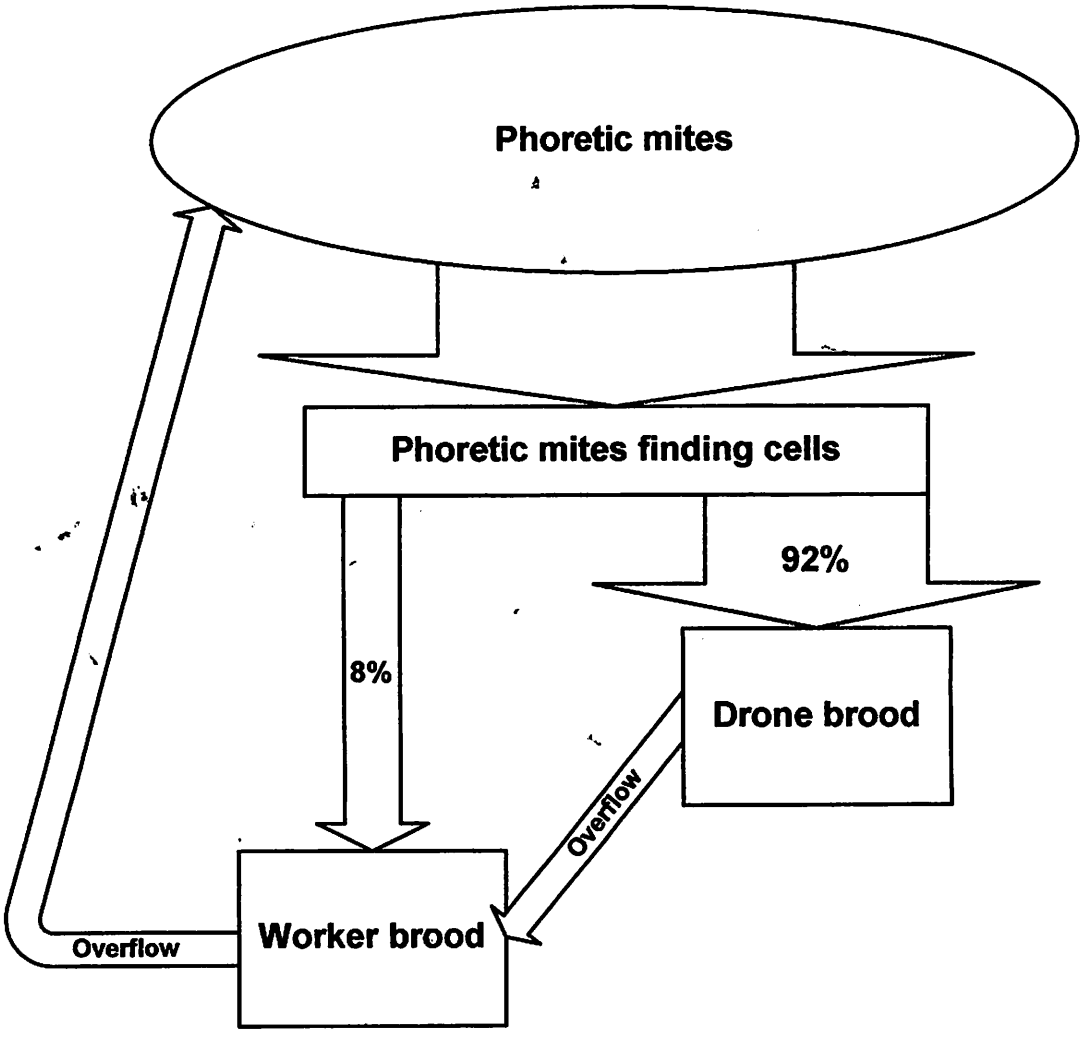

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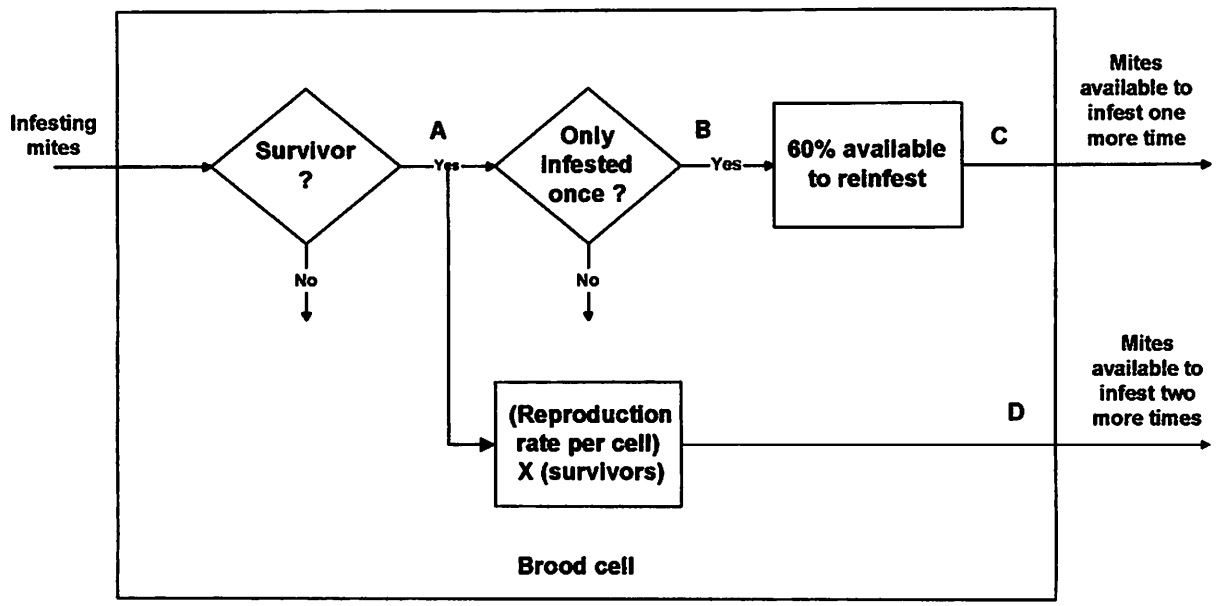


Fig. 3. Conceptual framework for estimating the number of mites able to infest brood cells each day in a honeybee colony.

On the day that a cell will be sealed, it becomes a candidate for infestation. Mites invade worker and drone brood at rates according to the functional response equation described in Calis *et al.* (1999) (Table 1) that predicts the proportion of phoretic mites that infest brood cells as a function of the number of phoretic mites, colony size and available brood cells.

Mites have a propensity to infest drone brood over worker brood at a ratio of 92 to 8% (Boot *et al.*, 1995) (Fig. 2). When the infestation rate of drone cells reaches 7 mites per cell (Sulimanovic *et al.*, 1982), the remaining mites will infest worker cells. A maximum of 4 mites can infest worker cells. Once all available drone and worker cells are maximally infested, no more mites will infest brood that day. Mites that did not infest brood on a given day will be available to infest brood cells the following day.

The proportion of worker and drone cells that foundress mites can survive and successfully reproduce in is a variable that is initialized at the beginning of a simulation. The number of mated female offspring emerging from single-infested worker and drone cells is also initialized through menus at the start of a simulation. When the foundress mite emerges from a cell with the adult bee, 60% are able to infest a second cell before they die (Martin and Kemp, 1997). The total number of mites able to infest cells each day is the sum of 1) the number of mated female progeny emerging from cells, 2) foundress mites capable of infesting cells a second time, and 3) phoretic mites in the colony that did not find cells to infest the previous day (Fig. 3). Mites are distributed among the worker and drone cells that are of suitable age for infestation.

Values for the number of mated daughters produced per foundress female in single-infested cells are estimated as the product of the number of viable mated female offspring produced per foundress and the percentage of mites producing viable offspring. Multiple infestations of drone and worker cells affect both the mite's reproductive rate in the cell and the longevity of the emerging adult bee (DeJong and DeJong, 1983; Kovac and Crailsheim, 1988). The reproductive rate (mated female mites produced per foundress) in multiple-infested drone and worker cells is determined by equations derived from data reported by Donzé *et al.* (1996) (Fig. 4, Table1).

Phoretic mite mortality is estimated differently depending if miticides such as fluvalinate are included in the simulation. If miticides are not included, foundress mites emerging from cells that will not infest cells a second time or have already infested cells a second time are removed from the phoretic mite population. If mortality from fluvalinate is included, only phoretic mites are affected and the percentage removed from the population is specified according to the average daily mortality for the miticide and the number of days it is effective.

Immigration of mites into colonies - Mite populations can increase two ways. The first is through reproduction in honeybee colonies. The second is by immigrating into colonies either carried on drifting honey bee foragers or drones, or when workers rob weak hives that are dying due to mite infestations (Kraus and Page, 1995). In the latter case, thousands of mites can enter a colony over

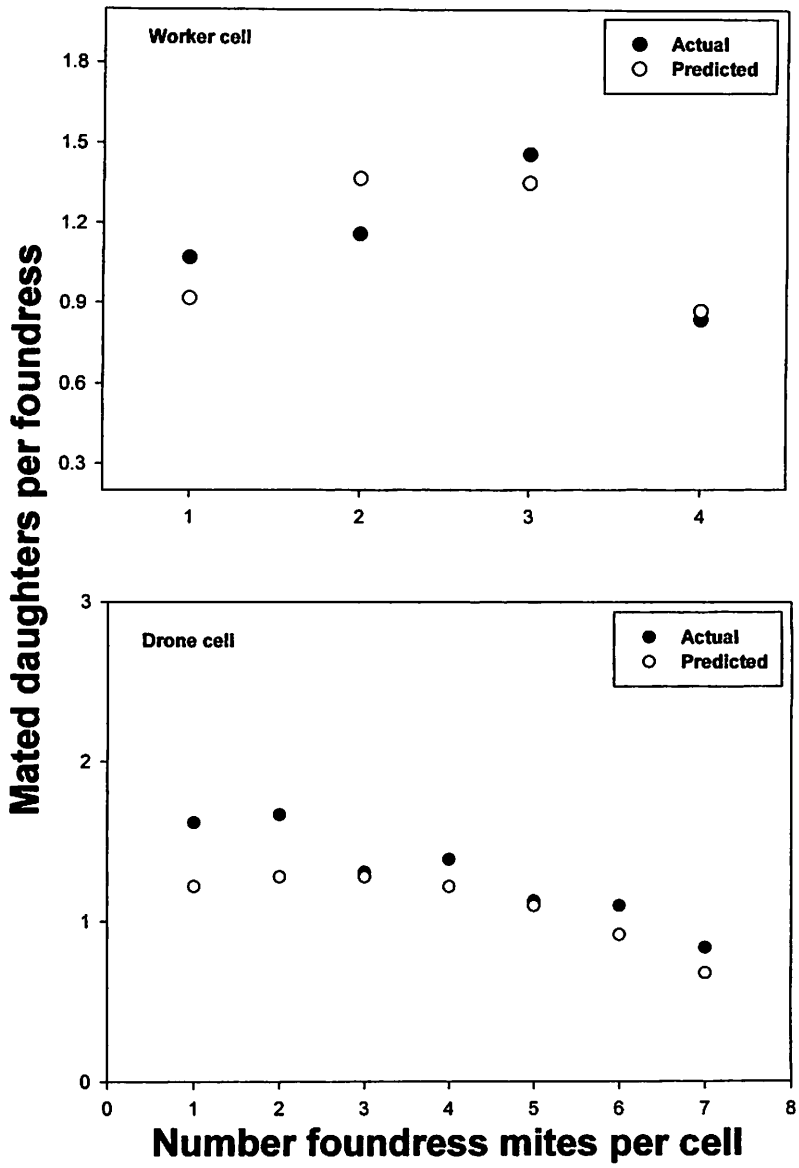
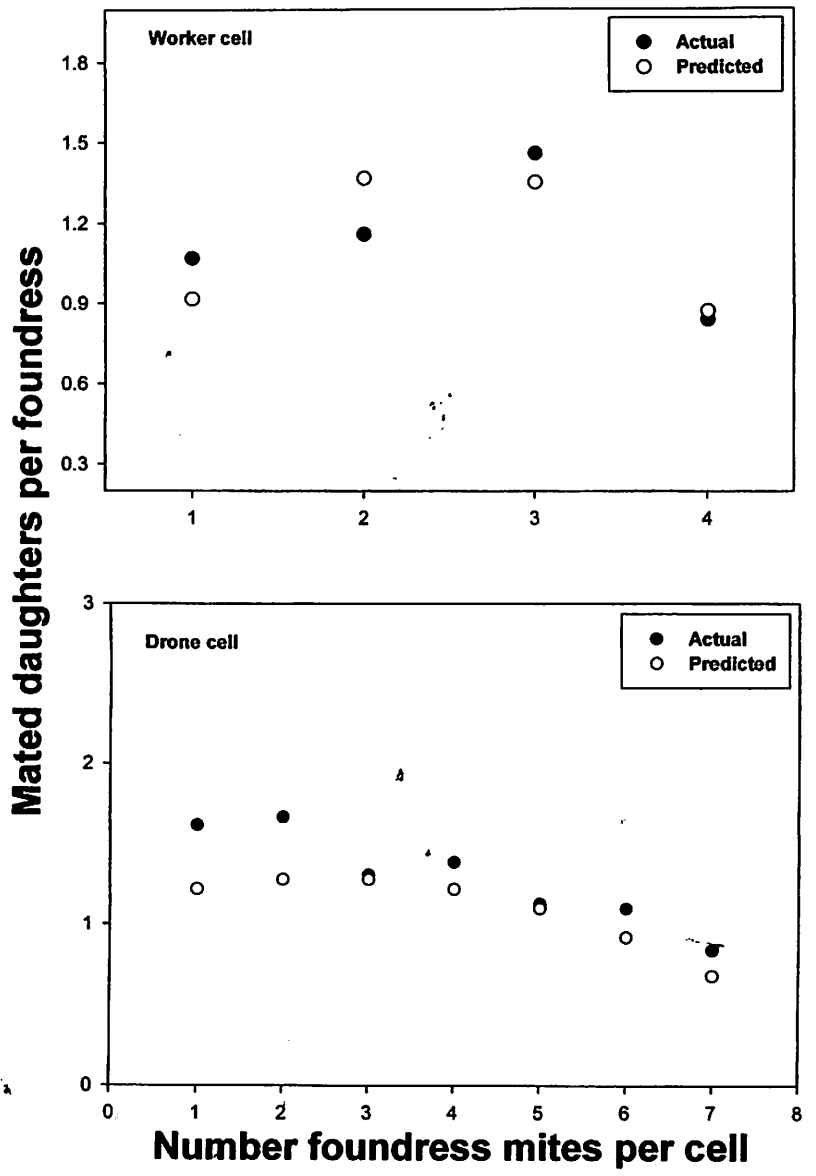


Fig. 4. Number of mated female mites produced per foundress in multiple-infested drone and worker cells as predicted by the model based upon equations derived from data (actual mated daughters per foundress) reported by Donzé *et al.* (1996).

a relatively short period of time and boost an otherwise modest mite population. Immigration of mated adult female mites into colonies is simulated by specifying the day that the immigration begins, the day it ends, and the number of mites that will enter the colony during that interval. A mathematical expression defining the immigration profile also can be specified. The proportion of immigrating mites that are resistant to particular miticides that may be included in the simulation also can be specified. It is assumed in the model that any immigrating mite is capable of infesting cells on the day it enters the colony. Thus, when the immigration option is activated, the total number of mites available to infest cells on a given day is estimated as the number of mated female mites emerging from cells, phoretic mites searching for cells, and those immigrating into the colony that day.

Application of miticides into the colony - Mite mortality from the application of miticides such as fluvalinate is simulated by specifying the date when the miticide is placed into the colony, the additional daily mite mortality rate caused by the miticide, and the number of days that the miticide remains effective. If fluvalinate is simulated, only phoretic mites on adult bees are killed. The proportion of the mite population that is resistant to the miticide also can be specified. Resistant mites are not affected by the miticide and are able to infest cells and reproduce. The progeny of the resistant mites are assumed to be resistant.



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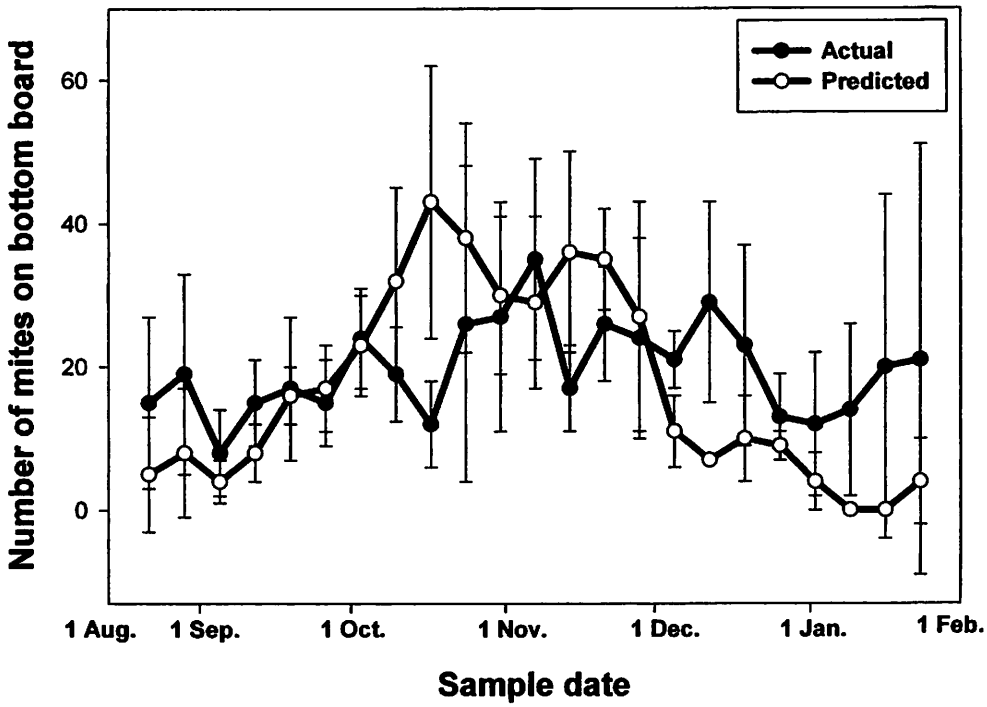

Fig. 5. The average natural mite drop per week in actual and simulated colonies ± 1.0 s.d. over a 23-week period from August to January.

Data collection for model validation - Five colonies (located at the Carl Hayden Bee Research Center in Tucson, Arizona) initially comprised of 3-4 frames of brood and 2-3 frames of honey and pollen were used for model validation data collection. The colonies had relatively low mite populations at the start of the trial as indicated by low numbers of falling mites on sticky boards prior to the start of data collection. A wire screen was set above each sticky board to prevent bees from contacting the sticky surface. The number of mites dropping on the sticky boards was counted weekly for 26 weeks starting on August 15, 2002. A new board was inserted each week. Simulations were conducted using Desert Southwest weather conditions (maximum and minimum temperatures = 39°C and - 6.7°C; hours of sunlight = 9.8 - 13.5; average wind speed =20.7 Km/hr, and 13 days with measurable rainfall) and initial mite populations ranging between 10-40 mites. The average number of mites counted weekly on the sticky boards was compared with weekly averages obtained from the simulations. The average mite drop per week in the simulated colonies was calculated by totaling the daily values for the number of foundress mites that emerged from brood cells and could not infest cells a second time plus the foundress mites that already had infested cells for a second time.

Two sets of mite-infested colonies (four colonies per set) were treated with fluvalinate to generate data for comparison with predictions from the model regarding mortality from a miticide. The first set of colonies was treated beginning on 20 September, 2001 and the second set on 6 June, 2002. In both cases, fluvalinate strips were left in the colony for 42 days. Weekly counts were made of the number of mites that dropped on to sticky boards placed on the bottom board of each colony. The percentage of the total mite population killed weekly in actual and simulated colonies was estimated by the equation: (mites killed in week(n) / total mites killed over 42 days) * 100%. Weekly averages estimated from the number of dead mites on sticky boards in actual colonies were compared with the weekly averages predicted by the model.

Conditions common to all simulations - A standard set of initial conditions was used in all simulations unless otherwise specified (Table 3). The conditions reflect an over-wintered colony building its population in the spring under either Temperate zone or Desert Southwest weather conditions. Under Temperate zone conditions, queens begin laying eggs in early February and continue until late October. The colony population peaks in July and August. Brood rearing ceases in the late fall until the following February. The colony population is comprised of only adult workers from November through January. Under Desert Southwest conditions, queens lay eggs throughout the year, but at a reduced level in the late fall and winter. Colony populations peak in July and August.

At the start of the simulation, queens are fully mated (5.5×10^6 sperm) and have the potential to lay 3000 eggs per day. The queen is removed and a new queen is added

Table 3. Initial conditions common to all simulations.

Parameter		*Value*
Initial colony size:	Eggs (worker)	5000
	Larvae (worker)	10000
	Adult worker	8000
	Adult drone	0
Capped brood:	Worker	8000
	Drone	0
	Adult workers	10000
	Adult drones	0
Percentage of capped brood infested with mites: Workers		10%
	Drones	0%
Percentage of adult bees infested with mites: Workers		10%
	Drones	0%
Mated female offspring produced by foundress mite single-infested [a] Worker cell		1.5
	Drone cell	2.7
% of mites that can successfully reproduce in[b] Worker cells		73%
	Drone cells	95%
Maximum number of eggs a queen can lay per day		3000
Forager life span		10 days
Starting date of the simulation		1 April

[a] Default values for mite reproduction in single-infested worker and drone cells are from Fries *et al.* (1994) and Martin (1998).
[b] Default values for the % of foundress mites that can successfully reproduce in single-infested worker and drone cells are from Schultz (1984 cited in Fries *et al.* 1994).

to the colony each year on September 1. We included a 10-day delay before the new queen begins laying eggs to simulate the removal of the old queen and the introduction of the new one. Resources and space are assumed to be unlimited. In all simulations, there is no mortality from miticides unless specified.

RESULTS

Comparison of actual mite drop data and model predictions - Estimates from the model were similar (i.e., within one standard deviation of the mean) to the average mite fall counted on the sticky boards in the experimental colonies from August through September (Fig. 5). The model predicted higher mite fall during the first two weeks in October, but predicted similar numbers to those in the colony from the third week in October through the middle of November. The model again predicted greater mite fall in late November and December than actually occurred. However, by early January the model predictions and actual mite fall were similar. The model predicted an increase in mite fall in January which agreed with actual counts from field colonies.

How do weather conditions in different geographic areas influence mite population growth and colony survival threshold levels? - Simulations were con-

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[a] Default values for mite reproduction in single-infested worker and drone cells are from Fries *et al.* (1994) and Martin (1998).
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to the colony each year on September 1. We included a 10-day delay before the new queen begins laying eggs to simulate the removal of the old queen and the introduction of the new one. Resources and space are assumed to be unlimited. In all simulations, there is no mortality from miticides unless specified.

RESULTS

Comparison of actual mite drop data and model predictions - Estimates from the model were similar (i.e., within one standard deviation of the mean) to the average mite fall counted on the sticky boards in the experimental colonies from August through September (Fig. 5). The model predicted higher mite fall during the first two weeks in October, but predicted similar numbers to those in the colony from the third week in October through the middle of November. The model again predicted greater mite fall in late November and December than actually occurred. However, by early January the model predictions and actual mite fall were similar. The model predicted an increase in mite fall in January which agreed with actual counts from field colonies.

How do weather conditions in different geographic areas influence mite population growth and colony survival threshold levels? - Simulations were con-

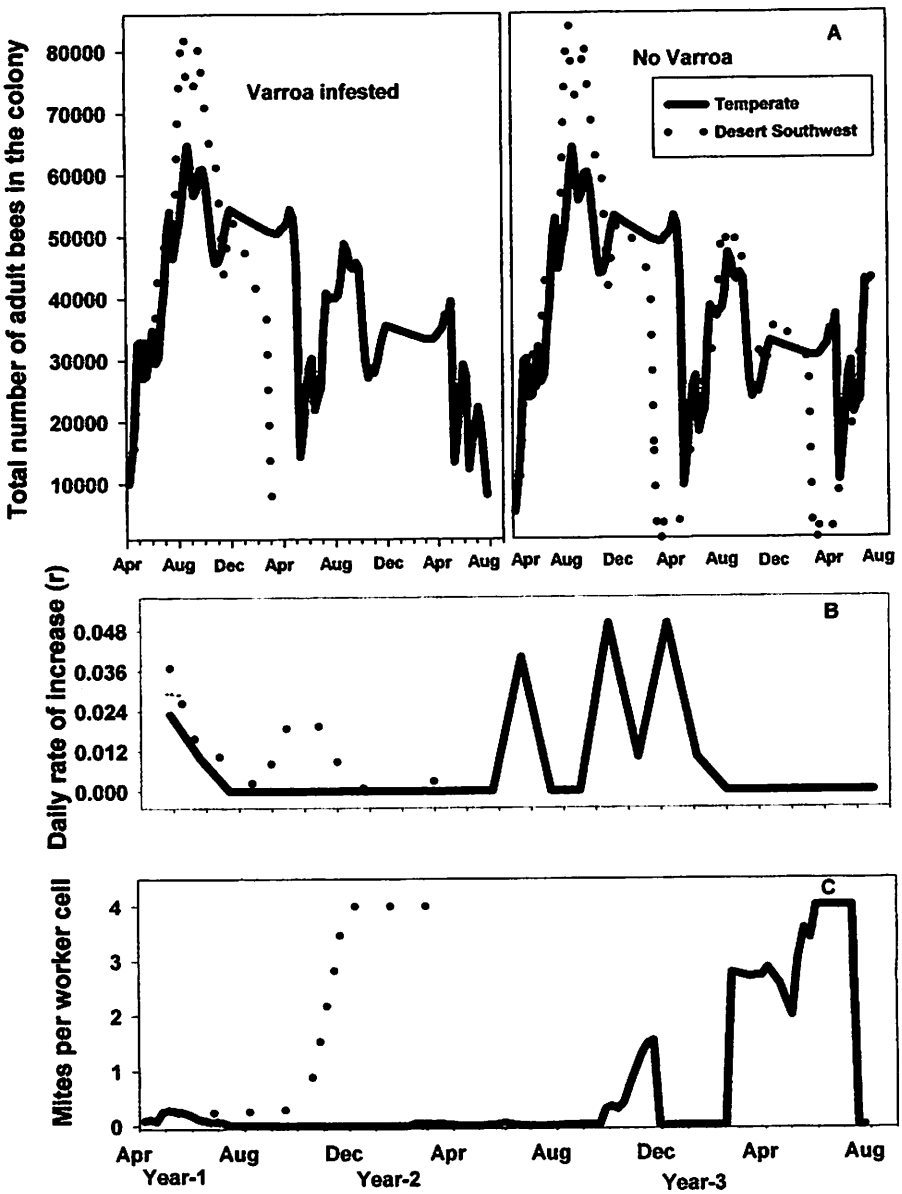


Fig. 6. Honeybee colony and *Varroa destructor* population dynamics (A), daily rates of increase under Temperate and Desert Southwest conditions (B), and average numbers of mites per worker cell (C) as predicted by the model. The daily rate of increase was estimated using the methods of Carey (1993).

ducted using standard initial conditions but with initial mite populations of 97 phoretic mites. The initial size of the mite population was based upon data indicating that honeybee colonies with populations of about 100 total mites in February would not survive unless treated with a miticide (Delaplane and Hood, 1999). To gauge the impact of mites on honeybee colony population growth, a separate set of simulations were conducted with the same initial conditions but without mite infestations.

Under Desert Southwest conditions, colony population growth was similar for simulations with and without mites until the spring of Year-2 (Fig. 6). The model predicted a decline in the colony population in the spring followed by an increase in the population that continued through the summer when there were no mites. However, in simulations with mites there were multiple-infested brood in the late winter and spring. Because workers emerging from multiple-infested cells have a reduced lifespan, the adult worker population declined and the colony was dead by April.

Under Temperate conditions, colony growth with and without mites was similar until the summer of Year-3. The colony with mites increased in size in May but not to the level of the mite-free colony which continued to increase throughout the summer. There were multiple infested worker brood cells throughout the spring and sum-

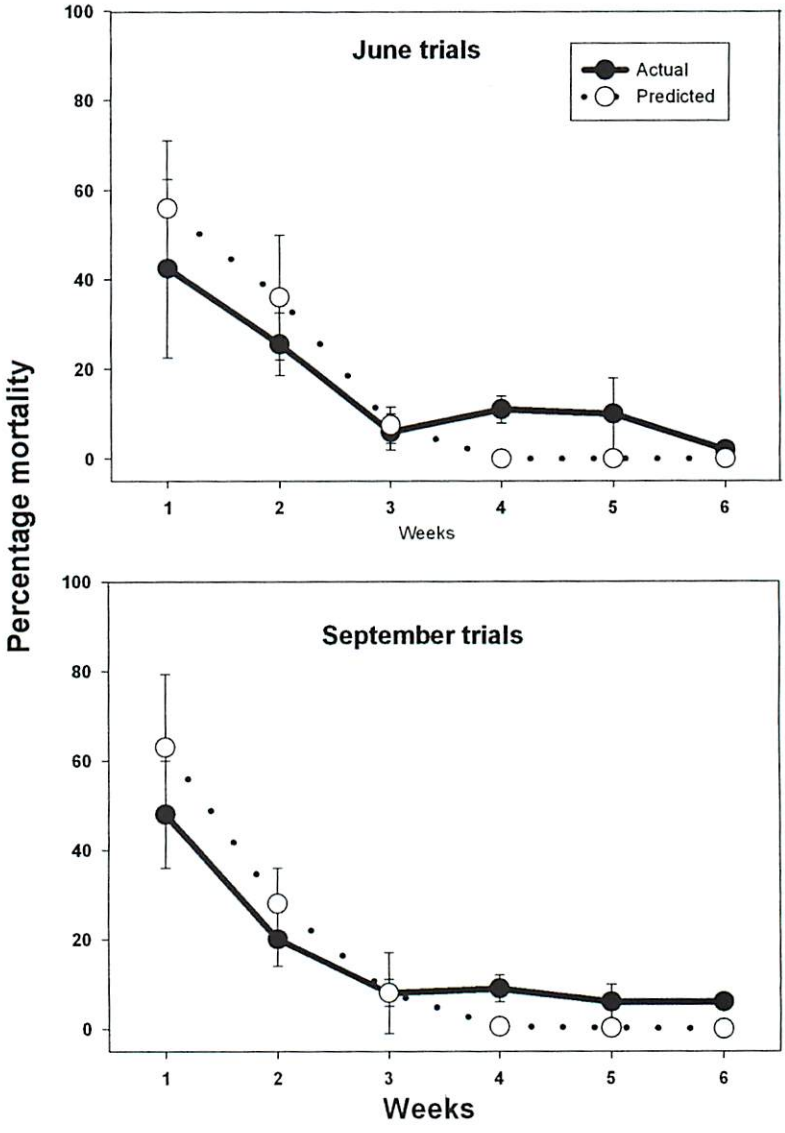


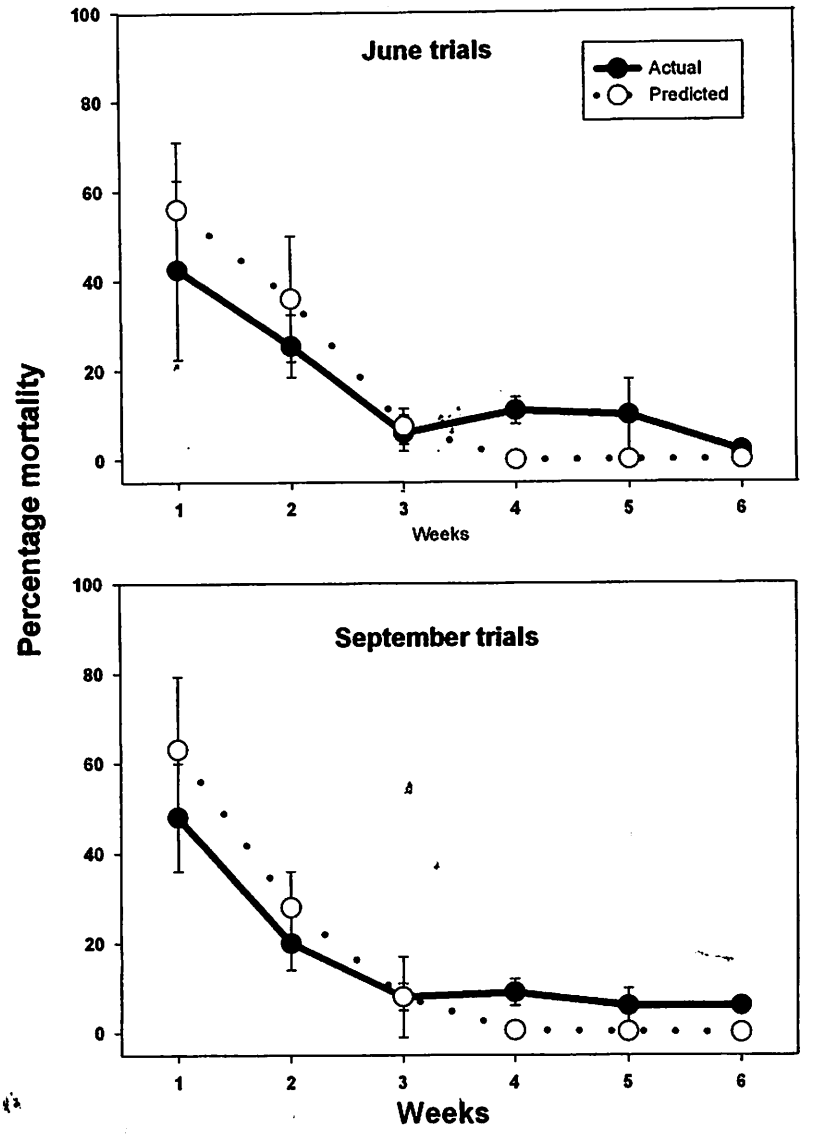
Fig. 7. Actual and predicted weekly percentages of the total number of mites killed by fluvalinate in actual colonies and predicted by the model. The weekly percentages were estimated by the equation: (total mites killed in week (n) / total mites killed during the 6 week treatment period) x 100%.

mer of Year 3, causing the adult worker population to decline due to reduced worker longevity. The colony was dead by August.

We conducted additional simulations under Temperate conditions to determine a colony survival threshold level in the spring that would cause colony death within a year. If the total population in February was ≥2500 mites, the simulated colony died in the spring of Year 2.

Using an initial value of 97 phoretic mites, we estimated the daily rate of population increase for the mite population (r) using the equation: $r = \ln (N_t / N_{t-1})$ where N_{t-1} = the number of mites in a colony yesterday and N_t = total mites in the colony today (Carey, 1993). In the model, the mite population growth rate (r) was higher in the spring for Desert Southwest conditions compared with Temperate conditions (Fig. 6). However, by June and July, r-values under both Temperate and Desert Southwest conditions were between 0.020-0.024. By October the mite population was growing exponentially, and there were multiple-infested worker brood cells by November. Since fewer mated female mites are produced in multiple-infested cells, the reproductive rate of individual females declined, as did r-values.

Under Temperate conditions, the mite population grew at a rate similar to that under Desert Southwest conditions until August when brood rearing and r-values declined. There was a rise in the mite population in Year 2 as growth rates cycled between 0.001 and 0.045. How-



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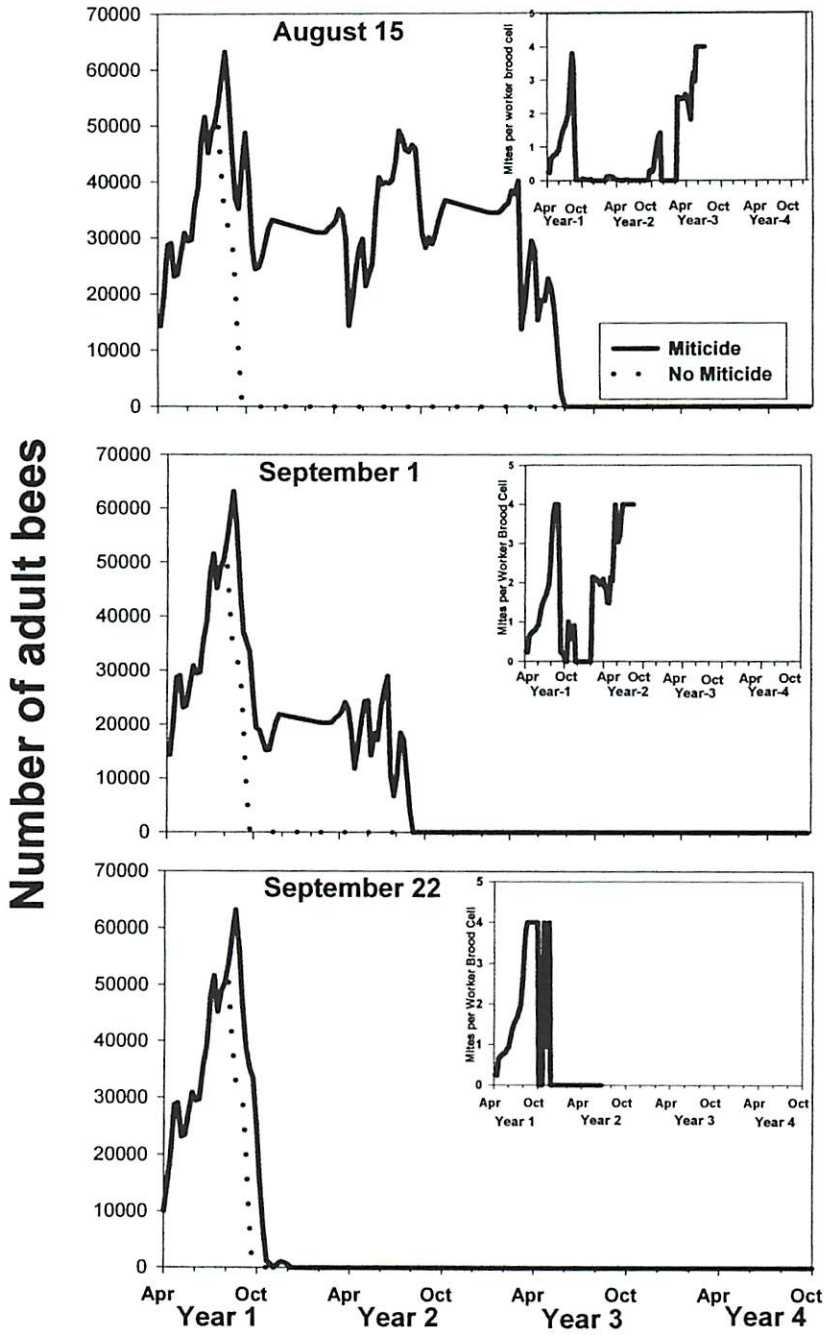

Fig. 8. Honeybee colony and *Varroa destructor* population dynamics with and without mortality from the miticide fluvalinate as predicted by the model. The miticide was simulated to kill 92% of the phoretic mites for 6 weeks. Mortality from fluvalinate was started on 15 August, 1 September or 22 September. The inset graph indicates the number of foundress mites infesting worker cells and when multiple infestations occurred that reduced adult worker longevity. Simulations were conducted using Temperate conditions.

ever, the growth rate again declined in the fall as brood rearing decreased. The mite population coming out of the winter of Year 3 increased rapidly in the spring. There were multiple-infested worker cells by late spring and r-values declined.

Does the timing of a miticide application impact colony survival?

Validation of model predictions with field data - We first conducted simulations using Desert Southwest conditions to determine whether model predictions of

mite mortality from fluvalinate were similar to those measured in the field. Mite mortality from fluvalinate did not differ between the June and September trials, so data were combined to obtain an average efficacy of 92.4 ± 3.3% mite mortality over the 42-day period. We set the mortality for the miticide in the simulated colonies at 92% of the phoretic mites. The initial mite population levels in the simulated colonies ranged between 1050-1418 adult females for the September trial (September average:1234 ± 184 mites) and 85-151 for the trial in June (June average: 118 ± 33.0). We began the simulations on 3 different starting dates; 15 June, 13 July, and 17 August for the simulations with a September miticide treatment and 8 March, 4 April, or 2 May for simulations with a June miticide treatment. Using different starting dates for a simulation resulted in variation among the simulations in both the numbers of mites in cells and on adult bees and the age distribution of bees in the colony. Three simulations were run for each starting date using an initial mite population equal to the average from the actual colonies or +/- 1.0 s.d. For each simulation, we calculated the percentage of mites that dropped weekly for the 6-week treatment interval. Average percentages of weekly mite drops predicted by the model were compared with actual percentages from the field trials.

During the first three weeks of treatment, there were no significant differences between actual and predicted mite mortality (Fig. 7). In the simulated colonies, nearly all of the mites were killed during the first three weeks. In the actual colonies, mite mortality in weeks 4-6 was low, but significantly greater than predicted by the model.

Fall miticide applications - The next set of simulations was conducted to determine if the timing of fluvalinate treatments in the fall affects colony survival. Simulations were run using standard initial conditions and with a starting date of 1 April. Colonies had initial populations of 3600 mites on 1 April. If mortality from fluvalinate was not included, the colony died in the late summer of Year 1. Simulations were conducted using Temperate and Desert Southwest conditions. Mortality from fluvalinate was set at 92% of the phoretic mites.

Similar results were obtained for both sets of weather conditions, so only those using Temperate conditions are shown. The length of time that the simulated colony survived depended upon when the miticide treatment began, and how much of the autumn brood were multiple-infested (Fig. 8). If mortality began on 15 August of Year-1, some worker brood was multiple-infested. However, when the mated female mites emerged, most were killed by the miticide. Consequently, the last brood cycles of the year had very few capped cells infested with mites. The simulated colony survived until the fall of Year 3 without additional miticide applications.

If mortality from fluvalinate began on 1-15 September of Year 1, the simulated colony survived for 2 years. The mite population decreased to nearly zero after the treatment but increased to the point where there were multiple-infested worker brood by the summer of Year 2. The simulated colony died in the fall.

When mortality from fluvalinate treatment began on 22 September or later, the simulated colony population was similar to that when no treatment was added. With miticide mortality starting in late September, nearly all of the worker larvae produced in the last brood cycle of the year were multiple-infested and the colony died by late November.

Spring miticide applications - In the next set of simulations, we applied a fluvalinate treatment in the spring to compare its effectiveness in insuring colony survival with the treatment beginning in the late summer. The simulations started on 1 January with either 1600 mites under Temperate conditions or 100 mites under Desert Southwest conditions. There were no eggs, larvae, or capped brood at the start of the simulation. Mortality from the miticide (92% of phoretic mites) began on February 15 and lasted for 42 days.

Under Temperate and Desert Southwest conditions, honeybee colony populations in simulations with treatment beginning in February were nearly identical to those where treatment began on August 15 (Fig. 9). If a February treatment was simulated, the mites per worker cell dropped to near zero and remained at a low level (less than 1 mite per worker cell) throughout the rest of the year. Without a February treatment, the mite population grew with the honeybee colony population throughout the summer. If treatment began in August, the mite population dropped to the same level as in simulations with a February treatment. The simulated colonies went into Year 2 with nearly identical mite populations and the colonies survived without additional treatments until the winter of Year-3.

A final set of simulations was conducted using Desert Southwest conditions to compare effects of fluvalinate application in February with no treatment. A simulation where 2000 mites immigrated into the simulated honeybee colony beginning on 1 June and ending on 15 July was included. The simulation with immigration also had mortality from fluvalinate beginning on 15 February. In all simulations, the initial mite population at the start of the simulation (1 February) was 97 mites.

After the reduction in the mite population due to mortality from fluvalinate, the model predicted that by May the population in treated colonies (with and without immigration) was nearly the same as in untreated colonies (Fig. 10). The number of mites in worker brood cells over time was similar among the simulations and is not shown. However, there were fewer multiple infested drone cells in simulations that included miticide mortality compared with those without mortality from miticides. When cells are multiple infested, each female produces fewer offspring. The higher mite reproductive rates of single-infested drone cells in the simulations with mortality from miticides caused the population to increase so that from May onwards total mites in the untreated and treated colo-

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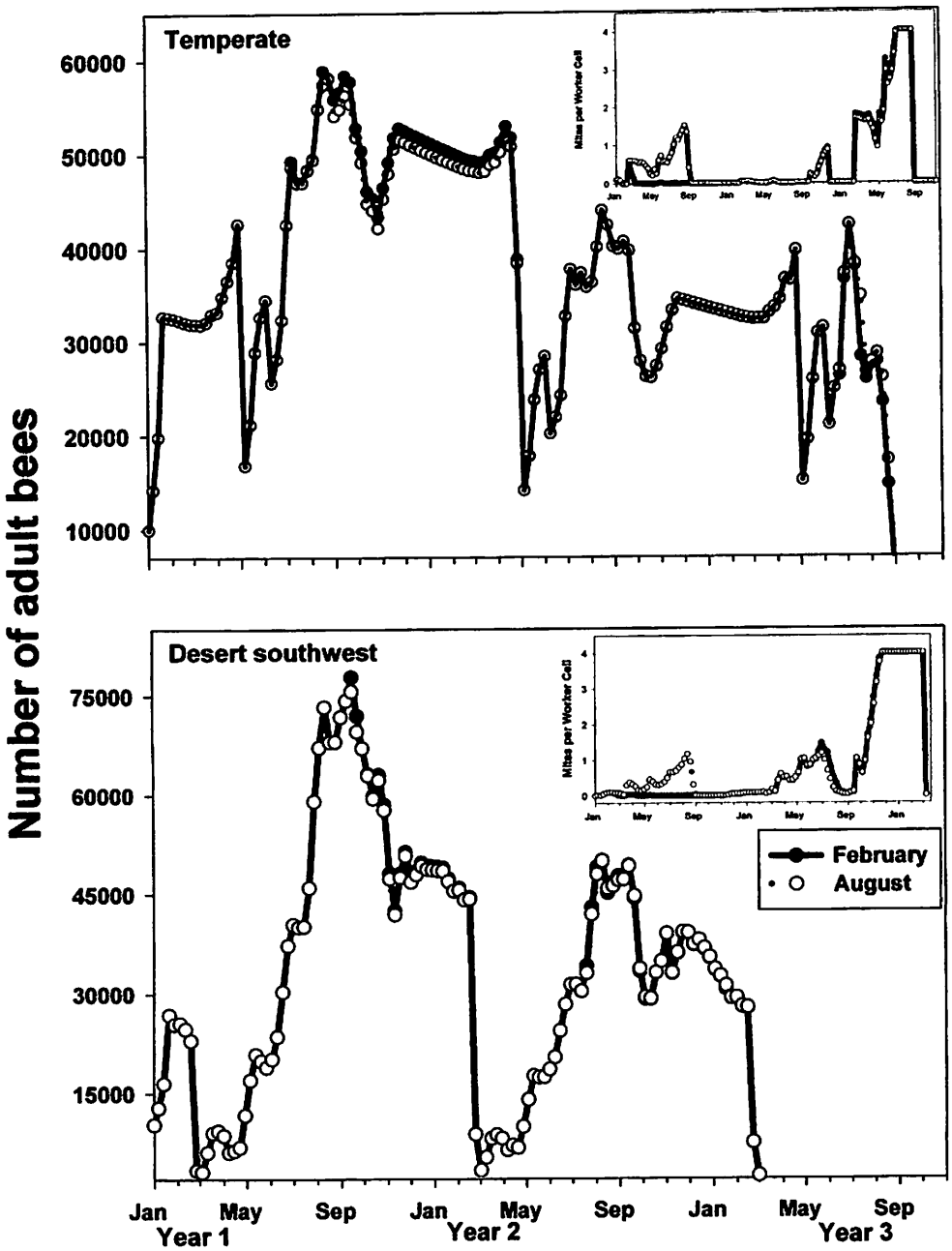


Fig. 9. Comparison of honeybee colony and *Varroa destructor* population dynamics when mortality from the miticide fluvalinate was started on either 15 February or 15 August. The miticide was simulated to kill 92% of the phoretic mites for 6 weeks. The inset graph shows the number of foundress mites infesting worker cells and when multiple infestations occurred that reduced adult worker longevity. Simulations were conducted using either Temperate or Desert Southwest conditions.

nies were the same. In the simulation that included immigration, more drone cells were multiple infested in June and July and the mite population growth rate decreased. By October though, the mite population was similar in all three simulations.

DISCUSSION

The model demonstrates how population growth of honeybee colonies and mite populations are dependent on weather conditions, seasonal brood rearing patterns, and mite infestation rates in worker and drone cells. The simu-

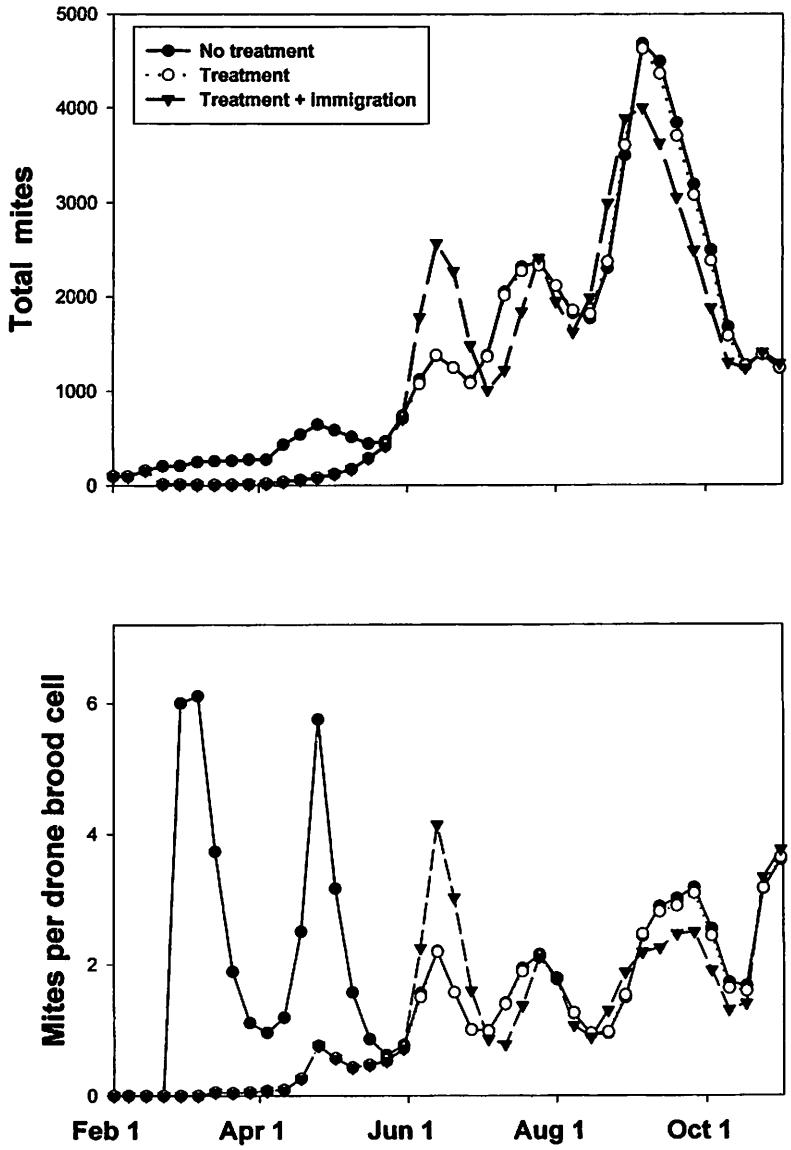
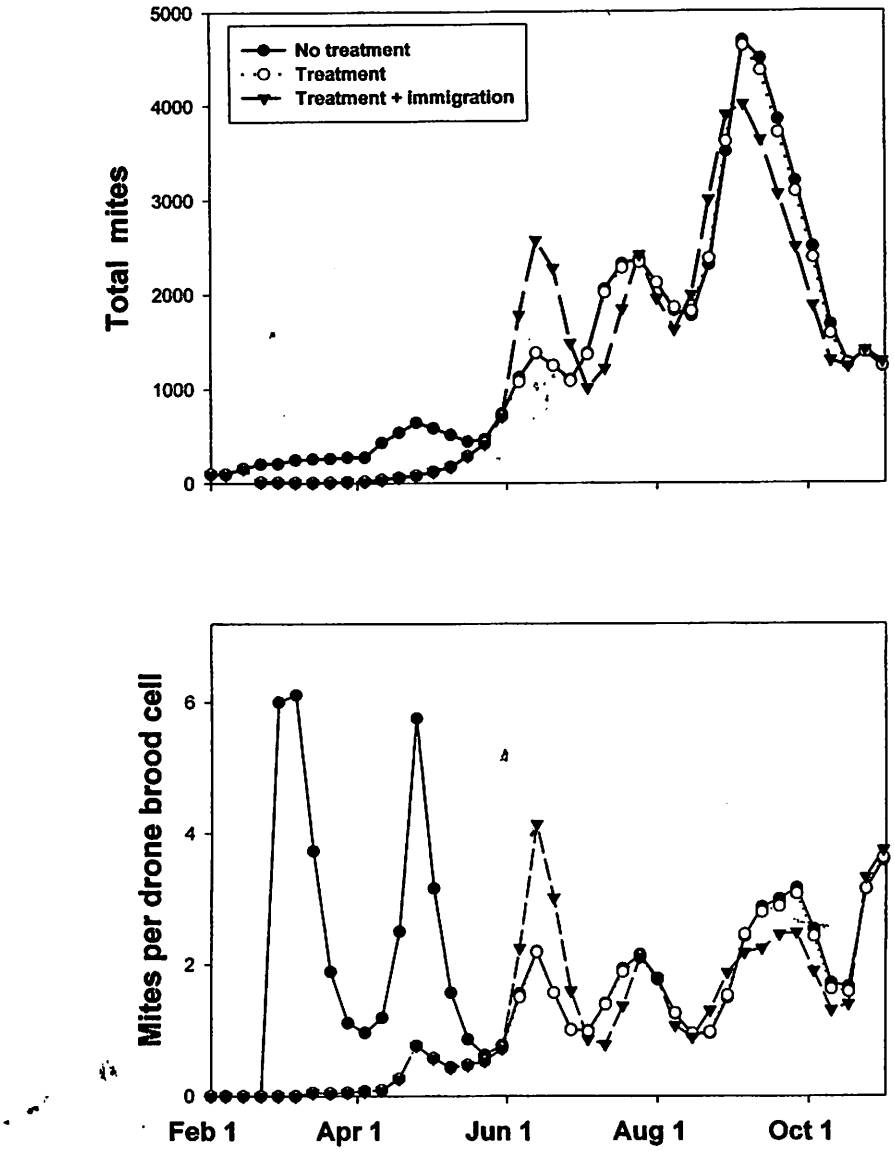


Fig. 10. *Varroa destructor* population growth and the mean number of mites per drone cell with and without mortality from the miticide fluvalinate. Mortality from the miticide was started on 15 February. The miticide was simulated to kill 92% of the phoretic mites for 6 weeks. Simulations were run using Desert Southwest conditions.

lations indicate that the effects of mites on adult worker longevity alone can determine the survival of honeybee colonies. The model also predicts that applications of miticides such as fluvalinate have a better chance of insuring colony survival if they are applied in late summer rather than later in the fall, and that the effectiveness of spring applications is mitigated because the surviving mite population increases as the colony population builds.

The model generated predictions on the daily rate of increase for the mite population and the importance of drone brood on population growth that were similar to previous models (Calis *et al.*, 1999, Wilkinson and Smith, 2002) and field trials (Kraus and Page, 1995). In colonies (Calatayud and Verdu, 1995; Kraus and Page, 1995; Martin and Kemp, 1997) and in a simulation model by Martin (1998), the daily rate of increase (r) in the mite population when brood is available is 0.021-0.025. Our model predicts daily rates of increase that vary from 0.022-0.029. Our model also predicts that mite populations will grow at a greater rate under Desert Southwest conditions compared with Temperate conditions because there is an uninterrupted brood cycle. Predictions that a longer brood rearing period dramatically increases the mite population were reported previously in models by Martin (1998; 2001); Calis *et al.* (1999); and Wilkinson and Smith (2002).



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The rate that mite populations increase in different climates affects colony survival threshold levels. The model predicts that when brood rearing is uninterrupted in the fall and winter, a spring mite population of about 100 total mites is sufficient to kill the colony within one year. The 1-year survival threshold for regions with uninterrupted brood rearing generated from field data is 97 mites (Delaplane and Hood, 1999). However, in Temperate climates where brood rearing stops in the late fall and winter, the model predicts higher survival threshold values. These results suggest that programs to control mites and estimates of survival threshold levels must be specific for geographic regions and take into consideration the annual brood rearing cycle of a colony.

Mite population growth and colony survival are interdependent. Once mite populations reach high levels, their rate of increase declines because in multiple-infested cells female mites do not achieve their reproductive potential. However, multiple infestation of worker brood predicates the demise of the colony because it shortens worker lifespan and compromises the population age structure. As demonstrated in actual colonies, predictions from our model and that of Martin (2001), colony survival is dependent not just on the number of adult workers but also the demographics of the colony population.

The model accurately predicted mortality rates for the first three weeks after a fluvalinate treatment. However, actual colonies treated with fluvalinate had greater mite drop during the last three weeks of the trial than predicted by the model. If a miticide kills 92% of the phoretic mites that are exposed to it, the model predicts that by the fourth week after the treatment, all susceptible mites have been exposed to the miticide and are gone. However, in the actual colonies we continued to find mites on sticky boards for the entire treatment interval, possibly indicating a continuous low-level immigration of fluvalinate susceptible mites into our colonies. Our test colonies were in an apiary with numerous nucleus and full-sized colonies, so drifting of worker bees carrying phoretic mites was quite likely.

Simulations indicated that the timing of fluvalinate applications, particularly in colonies with mite populations above survival thresholds levels, is critical to their effectiveness. In simulation, the optimum timing of an application hinged upon preventing multiple infestations of worker cells that comprise the last brood cycles before egg laying slows or stops in the fall. The model predictions of mite populations following February applications of fluvalinate were similar to those by Delaplane and Hood (1999), who reported that colonies treated in February had mite populations that were similar by September and October to untreated colonies. The results were partially attributed to the immigration of mites into treated colonies throughout the spring and summer. In our simulations, fall mite populations with or without fluvalinate treatment in February were similar whether immigration was included. This was because of reproduction in drone cells. In simulations without February treatment, there were multiple infested drone cells and mite population growth rates decreased. When the mite population was reduced in February due to a miticides application, there were single-infested drone cells during the spring and early summer and this generated higher rates of mite population growth. These simulations provide an alternative explanation to the limited effect that fluvalinate treatments in February can have, and highlight the importance of drone brood in augmenting the rate that mite populations can increase.

Other models of *Varroa destructor* population dynamics have been constructed (Fries *et al.*, 1994; Martin, 1998, 2001; Calis *et al.*, 1999). The main difference between our model and those of others is that our model predicts the impact of mites on colony survival due to the effects on worker longevity and colony demographics. Other models either did not predict the impact of mites on colony survival (Fries *et al.*, 1994; Martin, 1998; Calis *et al.*, 1999) or based predictions of colony mortality on the transmission of viral pathogens by mites (Martin, 2001). Our model also has functions to simulate requeening, immigration of mites into colonies, and the application of miticides.

A limitation of our model is that it does not simulate mortality factors such as disease transmission by mites. There is evidence for the role of *Varroa destructor* as a predisposing factor and vector of honeybee pathogens (Ball and Allen, 1988; Abrol, 1996; Bowen-Walker *et al.*, 1999; Brødsgaard *et al.*, 2000; Bakonyi *et al.*, 2002). Consequently, simulations covering a three year time period without treatment can generate predictions of mite populations before the colony collapses that might be unrealistically high. However, predictions on when the mite population would reach an exponential growth phase corresponded to previously reported accounts and are probably the best predictor of when an untreated colony might die from mite infestation.

Future work with the model will be directed at adding modules that could help screen possible controls for mites. For example, the feasibility of microbial agents such as fungi that might be used to reduce mite populations might first be evaluated in simulation. New miticides also could be evaluated especially if they cause lower mortality than those currently being used. The number and timing of applications that would be required to insure colony survival could be approximated in simulations and then tested in the field for accuracy. The model also could be used as a tool to manage resistance to miticides in a colony. For example, if low level resistance is occurring, the length of time before the mite population is no longer significantly reduced by the miticide in different geographic areas and brood rearing conditions, could be estimated.

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