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A population model for the ectoparasitic mite *Varroa jacobsoni* in honey bee (*Apis mellifera*) colonies

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Abstract

The ectoparasitic mite *Varroa jacobsoni* Oud. presently poses one of the most serious problems faced by keepers of honeybees *Apis mellifera* L. To help understand why the mite has become such a serious problem a population dynamics model using recently published data has been constructed. The simulation model has been built by linking together various aspects of the mites' biology using computer software (ModelMaker[®]) in such a way that an initial population of mites can change daily over any period. The model predicts a yearly 12-fold increase in mite numbers or an intrinsic rate of daily increase of 0.021 during the presence of bee brood. This corresponds well with field data. Values derived from the model for behaviours such as drone preference (5.5–12 times) and phoretic period (4–11 days) are similar to those actually observed. Therefore, the model can be used to predict the number of mites within any colony and their subsequent development over any period. Since the daily development of both the live population and numbers of dead mites are predicted by the model it can be used as a mite population monitoring tool. The model predicts that the ratio of live to dead mites will change dramatically between periods when bee brood is present or absent. However, since the ratios were shown to be stable within the periods, the mite population can be estimated throughout the year by multiplying the daily mite drop by ≈ 250 –500 or 20–40 when brood is absent or present, respectively. This will allow beekeepers to optimise their mite control strategy. The model also reveals the complex pattern in infestation levels that occurred throughout the year which was caused by the interactions between the bee and mite breeding cycles and will allow the role of bee viruses in the collapse of the colony to be studied in much greater detail. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: *Varroa jacobsoni*; *Apis*; Population; Model

1. Introduction

The ectoparasitic mite *Varroa jacobsoni* Oud. presently poses one of the most serious problems

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faced by *Apis mellifera* L. beekeepers. The first *A. mellifera* colony losses attributed to the mite occurred in the 1960's, in China and east Russia (Smirnov, 1978) and subsequently the mite has spread rapidly to all areas where *A. mellifera* bees are kept, except Australia and New Zealand. World-wide, the mite has caused the loss of many managed colonies with reported losses of 100000 in Argentina (Dietz, 1986), 300000 in Spain (Gomez Pajuelo, 1988), and 2 million in Poland (Hartwig, 1994). Also feral colonies have been decimated in many regions e.g. 75% loss in California (Kraus and Page, 1995a) and 71% loss in S. Arizona (Loper, 1995).

The female mite reproduces within the honey-bee sealed brood cell, which it invades just prior to it being capped. After cell capping the mite feeds on the developing bee and lays a single male egg followed by several female eggs at regular (30-h) intervals (Martin, 1995a). The eggs hatch and the offspring feed at a site established by the mother mite on the bee (Donzé and Guerin, 1994), mature and mate within the cell. The mature female mites leave the cell when the host bee emerges, with the males and any immature female mites quickly dying, since they cannot survive outside the sealed cell. Outside the cell (phoretic phase) the adult female mite lives attached to the adult bee where it feeds regularly on the bee's haemolymph by piercing the host's intersegmental membrane (Bowen-Walker et al., 1997).

Although colonies of the mites' original host *A. cerana* F. are normally found to be infested (Rath, 1991), the mites' population growth is limited by the bees' behavioural and physiological adaptations (Boecking and Ritter, 1994). These mechanisms are lacking in *A. mellifera*, thus allowing the mite population to increase freely until, if no action is taken by the beekeeper, the colony collapses. This takes 1–3 years depending on the initial infestation level. In order to maximise any mite control strategy estimates of the current and future mite population in a bee colony are required. A simulation model would provide such information. However, despite the importance of this parasite there has only been one previous attempt to model the complete population dynamics of *V. jacobsoni* (Fries et al.,

1994). That study was based on a review of the literature and identified several major gaps in our knowledge which would significantly affect the accuracy of any model predictions. The most important gaps concern the number and viability of the mite offspring. Studies aimed at filling most of these gaps have now been completed (Martin, 1995a,b; Lobb and Martin, 1997; Martin et al., 1997; Martin and Kemp, 1997) and along with new data from other studies (Boot et al., 1994, 1995a), it is now possible to construct a more realistic population model. This will allow better advice to be given to beekeepers and provide a valuable tool for *Varroa* researchers.

This paper presents the model parameters and construction, compares its predictions with field data and discusses its use as a monitoring tool.

2. Materials and methods

The model has been constructed by breaking down the mites' life cycle into compartments, each of which represents a measurable quantity, e.g. number of eggs laid, offspring mortality, etc. The compartments are then linked together using computer software (ModelMaker[®], 1994) in such a way that an initial population of mites can change daily depending on the current conditions, in a realistic way. Fig. 1 gives the basic model structure. In the following text all parameters discussed and used in the model are shown in bold.

2.1. Model elements

2.1.1. Honey bee colony

The numbers of adult worker bees, worker and drone brood (eggs, larvae and pupae) throughout the simulation period are required. Brood data from Allen (1965) and adult bee data (Martin, unpublished) from a colony with similar amounts of worker brood to that of Allens' study were used. The model interpolates between inputted data to calculate the daily number of bees and brood, shown graphically in Fig. 2. It is assumed for simplicity, that the mite population has no effect on the honey bee colony so the same colony data can be used in subsequent years.

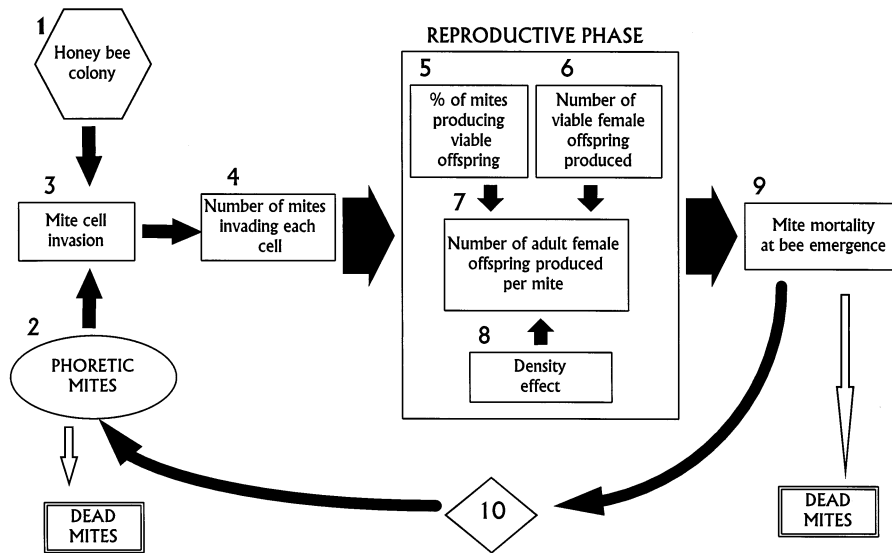


Fig. 1. Basic model structure of the *V. jacobsoni* life-cycle. The numbered compartments refer to the various model elements.

Daily rates of egg-laying or cell-sealing are calculated by dividing the number of brood present on that day by its developmental period, which for *A. mellifera* in UK conditions is **492 h** (20.5 days) or **576 h** (24 days) for worker or drone brood respectively. The duration of the sealed brood period was set at **282 h** (11.75 days) or **360 h** (15 days) for worker or drone brood respectively (Martin, 1994, 1995a).

2.1.2. Phoretic mites

While on the adult bee the mite dies, either naturally or is removed by the grooming behaviour of the bees. The mortality rates during the phoretic period have been measured indirectly by several studies and were found to vary widely (Table 1).

The mean daily rate of mite mortality during the winter for the 35 colonies studied was **0.002** mites per day and **0.006** for the three studies conducted when brood was present. The higher summer value probably reflects more bees and their mites dying away from the hive due to the increased foraging activity. Any mites removed by grooming are included in the post-emergence mite mortality rates, since previous

studies (Fries et al., 1996; Martin and Kemp, 1997) showed that the majority of mites are removed within the first 24 h.

There is an assumption in model development that there is no dispersal of mites from, or invasion to, the colony. However, when reliable data becomes available, this parameter can easily be incorporated by either adding (invasion) or removing (dispersal) mites to or from the phoretic mite element.

2.1.3. Mite cell invasion

Studies by Boot et al. (1994, 1995a) indicated that the rate of mite invasion into brood cells was related to the amount of brood and adult bees present. Martin and Kemp (1997) confirmed this finding in the worker brood. So the equations of Boot et al. (1994, 1995a) are used to calculate the daily invasion rate. These are:

Logit(*P*)

$$= 0.00385 \times [\text{worker brood/bees ratio}] - 2.87,$$

Logit(*P*)

$$= 0.0235 \times [\text{drone brood/bees ratio}] - 2.02$$

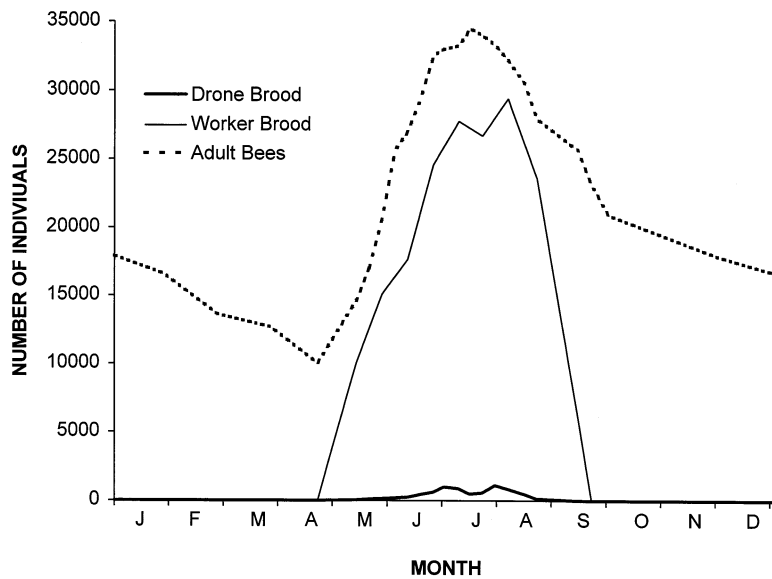


Fig. 2. The daily number of adult bees, worker and drone brood in the honeybee colony used by the model.

where (P) = probability of invasion, [brood/bees ratio] = number of suitable brood cells for mite invasion per kg (9000) of bees.

However, these studies were conducted with colonies that contained only one brood type, whereas in natural colonies both brood types normally exist, presenting the mites with a choice. The proportion of phoretic mites which invade each cell type could be based on the numerical proportion of worker to drone cells present on that day. However, *V. jacobsoni* is known to show a strong preference for drone brood (reviewed in Fries et al., 1994). This is due to several factors:

1. The period before cell capping when cells are invaded is 45 h for drone and 18 h for worker (Ifantidis, 1988; Boot et al., 1992). Therefore, a drone cell is suitable for invasion 2.5 (45/18) times longer than a worker cell.
2. There are 520 drone and 857 worker cells per dm² of comb (Dadant, 1975), so a mite has 1.648 (857/520) times more chance of encountering a drone rather than a worker cell.
3. Larval weight at cell sealing is 346 mg for a drone and 140 mg for a worker (Winston, 1991) so 2.47 times (346/140) more visits by the bees to a drone cell may be made.

4. Chemical factors may make the drone brood more attractive than the worker brood to the mite (Le Conte et al., 1989).

To allow for these factors the numerical proportion was adjusted to account for the longer invasion period (2.5 times), larger cell (1.648 times) and larger larvae (2.47 times) of drone brood. The attractiveness of drone brood due to a chemical factor is accounted for by the steeper curve produced by the equation of Boot et al. (1995a).

It is also possible to determine the proportion of mites entering either drone or worker cells by normalising the relative invasion rates calculated from Boot et al. (1995a) (Fig. 2). However, both techniques give similar results (see Section 4 for explanation), but the method given here allows for adjustment when new data becomes available.

Therefore, the equations to calculate the daily proportion of mites invading drone or worker cells are:

$$\frac{\text{daily number of drone cells} \times 2.5^2 \times 1.648^2 \times 2.47}{(\text{daily number of drone cells} \times 2.5 \times 1.648 \times 2.47) + \text{daily number of worker cells}}$$

for drone brood, and

Table 1

The daily phoretic mite mortality rates from various studies conducted during either winter or summer

Percentage of mites lost (a)	Number of colonies studied	Time of study	Study period (days) (b)	Daily mite mortality $1 - [(1 - a/100) \wedge 1/b]$	Author
13.6 ± 8.5	25	Winter	125	0.0012	Moosbeckhofer, 1991
40 ± 20.7	10	Winter	125	0.0041	Korpela et al., 1992
		Summer		0.006	Boot et al., 1992
	5	Summer	10	0.0045 ± 0.0017	Martin and Kemp, 1997
	6	Summer	10	0.0076 ± 0.0051	Martin and Kemp, 1997

1 – (proportion available to invade drone cells)

for worker brood.

Thus, the daily number of mites invading worker or drone cells is:

phoretic mites

× proportion invading drone or worker brood

× probability of invasion

2.1.4. Number of mites invading each individual cell

Since mites invade both worker and drone brood cells randomly at any constant infestation level (Martin, 1995b), and we know both the number of invading mites and number of suitable cells for invasion, it is possible to calculate the number of cells invaded by 0, 1, 2, 3 or 4 mother mites using the Poisson distribution:

$$((\exp(-m) \times m^z) / z!)$$

× number of available cells

where m = daily number of mites invading worker or drone cells/daily number of available worker or drone cells, z = number of mites invading the cell.

If there are fewer than 100 worker or ten drone cells no cell invasion takes place as this avoids the creation of artificially high values of 'm' occurring.

2.1.5. Percentage of mothers producing viable female offspring

Not all mites invading brood cells are able to

produce viable female offspring. This is due to a variety of reasons:

1. Death of the invading mites within the cell, normally before any eggs are laid. This occurs at a rate of 1.5–2% in worker cells (Kustermann, 1990; Martin, 1994) and 7.7% in drone brood (Martin, 1995a).
2. Females may be unfertilised due to the premature death of the male (Martin et al., 1997) or have exhausted their egg or sperm supply. These non-reproducing mites consist of 3.3% in drone (Martin, 1995a) and 5% in worker cells (Martin, 1994).
3. Females may fail to reproduce due to 'behavioural infertility' although they are fully capable of doing so. This has been found in studies (7%, Ruijter, 1987; 4%, Martin et al., 1997) where known individuals have been followed through subsequent reproductive cycles. Seasonal (Otten and Fuchs, 1990) or nutritional (Rosenkranz et al., 1988) factors may play a role.
4. Females produce only male offspring. This phenomenon occurs within $\approx 9 \pm 8\%$ of the mite population (Martin et al., 1997).
5. Females produce non-viable eggs, these are normally haploid (male) Akimov et al. (1990) and may be due to a lack of sperm. Rates of 8% in worker and 4.4% in drone cells have been recorded (Martin et al., 1997).

Combining all of these factors results in $\approx 30\%$ of the mite population producing no or non-viable female offspring.

A large number of studies have measured the percentage of fertile mothers in the population

Table 2
Percentage of fertile mites recorded by various studies excluding Africanised bees

Author	Worker	Drone	Type of data	Adjusted worker ^a	Adjusted drone*
Various review in Fries et al., 1994	86.6 ± 5.3, 12 studies	96 ± 3.2, 3 studies	Inc. mites producing only males and non-viable offspring	69.6	82
Various review in Martin et al., 1997	86.0 ± 5.9, 23 studies	92.5 ± 4.8, 4 studies	Inc. mites producing only males and non-viable offspring	69	78.5
Fuchs and Langenbach, 1989	71.5	63.1	Only adult female offspring	71.5	63.1
Ifantidis, 1990	67.7	Only adult female offspring		67.7	
Schulz, 1984	73	95	Only adult female offspring	73	95
Martin, 1995a		55	Only adult female offspring		55
Martin, 1995b	52.8 ± 11, 5 studies		Only mated adult female offspring	67.8	
			Adjusted mean	69.8 ± 2	74.7 ± 14

The adjusted values represent the percentage of mites producing adult female offspring.

^a Adjusted values: single male, 9% worker and 9.6% drone; non-viable offspring 8% worker and 4.4% drone.

(Table 2). However, some have included females producing only male offspring and or non-viable offspring in their calculations and this will over-estimate the number of mites producing mature female offspring. Using current data it is possible to adjust the values from previous studies to allow for a more realistic comparison to be made. The adjusted mean percentages of mites producing viable female offspring are **69.8%** in worker and **74.7%** in drone brood (Table 2). Therefore, the remaining mites will produce no or non-viable offspring which corresponds well with the 30% arrived at above, but the figures based on the adjusted figures are used in the model since they are arrived at from a larger data set.

2.1.6. Number of viable female offspring produced per reproducing mite

All the following data are based on singly infested cells:

2.1.6.1. Number of eggs laid. It is normal for a fertile mite to lay five eggs (one male and four female) in worker cells and six eggs (one male

and five females) in drone cells (Martin, 1995a), although there is some small variation in the numbers.

2.1.6.2. Offspring survivorship. During the development of each offspring its survival rate depends on the time of egg-laying after cell sealing and host brood type (Martin, 1994, 1995a). The shorter development time of *A. mellifera* worker brood compared with the natural host of the mite (*A. cerana* drone brood), means that under normal conditions the 4th and often 3rd females fail to mature before bee emergence. The survivorship rates (Table 3) reduce the four female eggs laid to **1.45** surviving to maturity in worker and five female eggs laid in drone cells to **3.90** mature offspring. Although male offspring mortality results in a similar percentage of the adult female offspring being unfertilised and these mites do survive, invade cells and attempt to breed (Martin et al., 1997), they are not considered here as they become part of the non-viable pool of mites and so are accounted for in the percentage of non-viable mites.

Table 3
Survivorship of mite offspring in drone (Martin, 1995a) and worker (Martin, 1994) brood

	Male offspring	1st female offspring	2nd female offspring	3rd female offspring	4th female offspring	5th female offspring	No. of adult female offspring
Drone brood	0.88	0.98	0.94	0.84	0.76	0.38	3.90
Worker brood	0.85	0.94	0.38	0.13	0	0	1.45

Table 4

Percentage reduction in the mean number of offspring produced per invading mites as invasion grade increases

Invasion grade	<i>A. mellifera</i> drone $n = 3$	<i>A. mellifera</i> worker $n = 8$	<i>A. cerana</i> drone from Rath, 1991
One mite/cell	0 (1)	0 (1)	(0.905)
Two mites/cell	16 (0.84)	9 (0.91)	(0.286)
Three mites/cell	35 (0.65)	14 (0.86)	(0.143)
Four mites/cell	34 (0.66)	40 (0.60)	(0)

Based on mean values of 'n' studies reviewed by Martin, 1995b. The density factors used in the model are given in parentheses.

2.1.7. Number of viable adult female offspring produced per mite

The average number of viable female offspring produced per invading mite is calculated by multiplying the number of surviving mature female offspring by the percentage of mites producing viable offspring:

$$1.45 \times 0.698 = \mathbf{1.01} \quad \text{in worker cells and}$$

$$3.9 \times 0.747 = \mathbf{2.91} \quad \text{in drone cells.}$$

These values are consistent with those from others studies (Fries et al., 1994; Martin, 1994; Boot et al., 1995b; Donzé et al., 1996).

2.1.8. Effect of mite density in host cell

As the mite population increases, the probability of a cell being invaded by more than one mite rises, resulting in the number of offspring produced per mite falling due to possible competition at the feeding site (Fuchs and Langenbach, 1989; Martin, 1995b). This density effect is very important in controlling the development of mite populations in *A. cerana* (Rath, 1991; Martin, 1997a). However, in *A. mellifera* the effect of crowding is much less dramatic since much higher numbers of invading mites are needed to kill the host. The model uses data from previous studies (Martin, 1995b) to calculate the percentage reduction in the number of offspring produced relative to the level of invasion (Table 4).

2.1.9. Mite mortality associated with bee emergence

Mites falling to the hive floor during the emergence of the host bee consist of those that died within the sealed cells, failed to attach successfully to a bee or were removed by the grooming activi-

ties of the host. Studies have shown that the number of mites (adult females) falling during worker brood emergence increases by a factor of six (Lobb and Martin, 1997) or 7–15 (Martin and Kemp, 1997) above periods when no brood emerges. Around 50% of these mites, recorded daily, were still alive and represent 15–19% of the total live mite population that emerged from the worker cells (Martin and Kemp, 1997). The total proportion of the emergent mite population dropping daily during brood emergence was 30% (Martin and Kemp, 1997) which is similar to the 24% reported by Boot et al. (1995b). Although data do not exist for drone brood, it is known that the associated mite drop with drone brood emergence is lower than that from worker brood (Lobb and Martin, 1997) so an estimated 20% was used.

These rates of mortality determine the number of times each mite can reproduce during its life; it is assumed that the mortality rate is similar for each age class of mites (Fries and Rosenkranz, 1996). Obviously the length of the phoretic period between reproductive cycles will lower the mean value. However, a 30% loss of mites during each reproductive cycle, excluding any phoretic death, results in a mean number of reproductive cycles of ≈ 2.4 for mites reproducing in worker cells. This figure falls within the range found in other studies (reviewed in Martin and Kemp, 1997).

2.1.10. Linking the reproductive and phoretic compartments

In the model the mites which invaded cells and their subsequent offspring are held for the duration of the host sealed brood period by a delay function. Then the falling mites join the dead mite

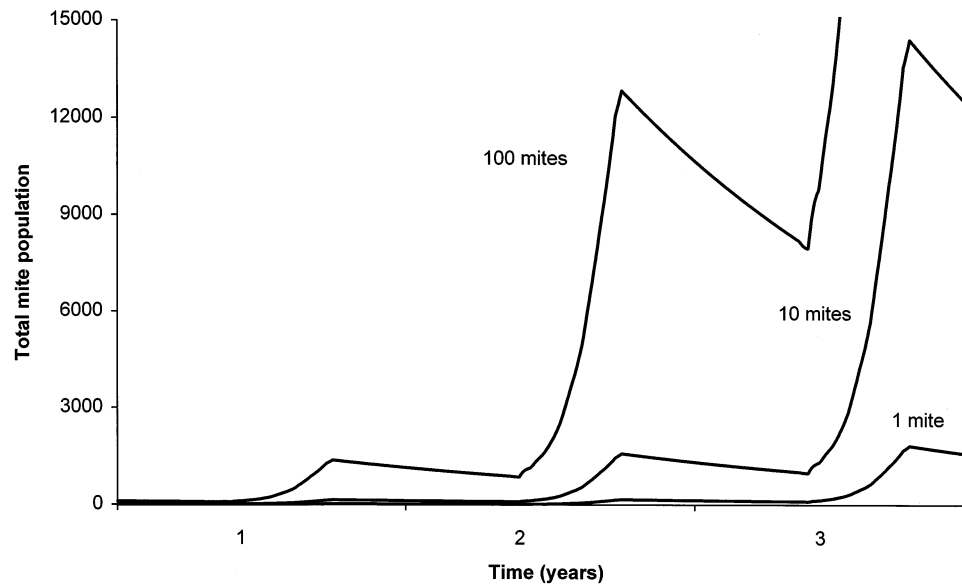


Fig. 3. Predicted mite population development over a 3-year period, when starting with different (1, 10 or 100) numbers of mites.

pool and the surviving individuals are added to the pool of phoretic mites where they are able to invade cells again when the right conditions prevail. All model runs were started on January 1st with ten phoretic mites and run for 3 years unless otherwise stated.

3. Results and discussion

3.1. Total live mite population

This consists of the phoretic mites plus the mother mites present in the brood cells. The growth in the mite population using different initial mite numbers is shown in Fig. 3. The daily rate of mite population increase during the presence of bee brood predicted by the model is 0.021. This is similar to that found in other studies (0.021, Calatayud and Verdú, 1995; 0.021, Kraus and Page, 1995b; 0.022–0.025, Martin and Kemp, 1997) indicating a realistic rate of mite population growth. Over the year the mite population increases 12-fold in this colony which has a 128-day breeding season. However, in areas where brood is continuously present, the model predicts a yearly increase of ≈ 800 -fold. These very large

increases were also predicted by Kraus and Page (1995b) in California where continuous brood is present.

3.2. Phoretic period

The phoretic period is determined by the amounts of brood and bees i.e. rate of invasion. To check the validity of this assumption the average phoretic period when bee brood is present was calculated. Fig. 4 shows that the predicted mean phoretic period varies between 4 and 6 days when there is brood present. Actual measured phoretic periods range between 4.5 and 11 days (reviewed by Fries et al., 1994). This confirms the assumption that the phoretic period is determined by the colony state.

3.3. Drone preference

This is the ratio of the number of mites invading drone cells to the number of mites invading worker cells. Studies (reviewed by Fries et al., 1994) show that the mite has a preference for drone brood of between 5.5 and 12.1 times that of worker brood. Fig. 5 shows the drone preference generated by the model is within the observed

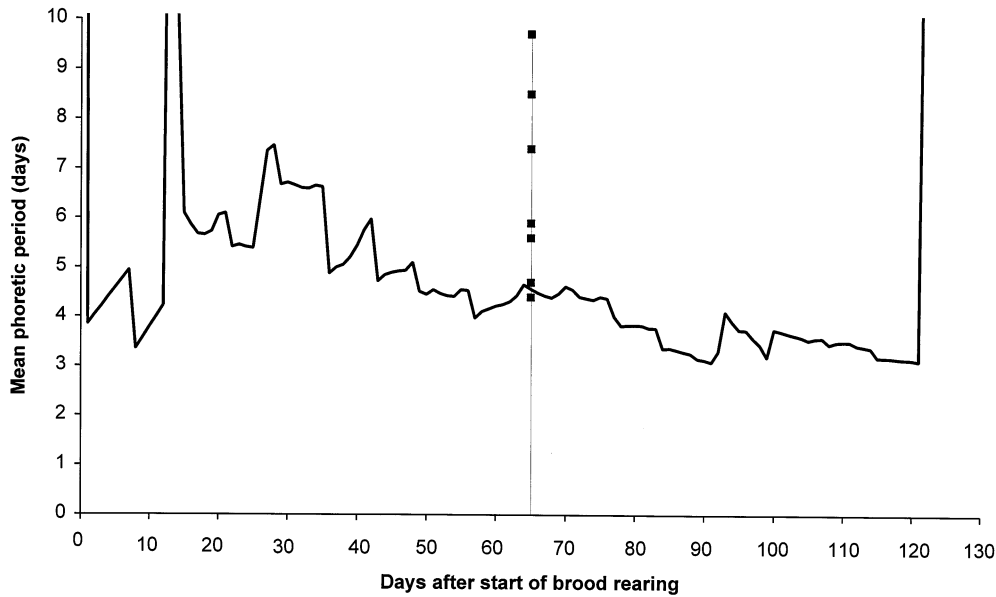


Fig. 4. Predicted mean mite phoretic period during the period when brood is present (line) and actual observed values (squares) from several studies (reviewed by Fries et al., 1994).

values, supporting the adjustments made to the numerical proportion of drone to worker cells (Section 2.1.3). If these adjustments are not made,

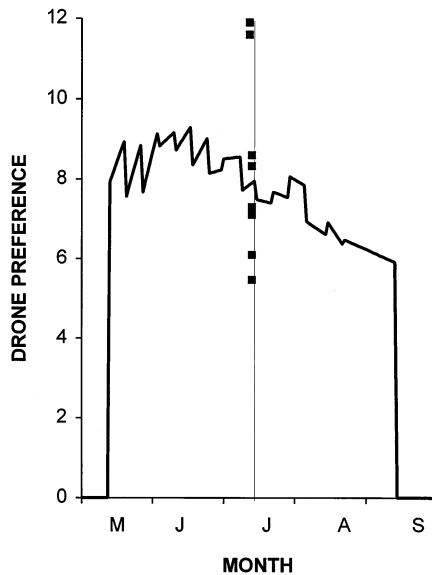


Fig. 5. Predicted drone preference shown by the mites (line) and actual observed values (squares) from several studies (reviewed by Fries et al., 1994).

the resulting drone preference is very low (1–2 times). Alternatively, if the number of invading mites was determined solely by the equations for each brood type without taking the proportion of brood types into consideration, the drone preference was unrealistically high (20–140 times). Furthermore, Boot et al. (1995a) showed that mites invaded drone cells 11.6 times more frequently than worker cells. This frequency can be almost explained in terms of the longer invasion period, larger larval and cell size of the drone ($2.5 \times 1.65 \times 2.47 = 10.2$). This suggests that the role of any chemical factors (Le Conte et al., 1989) above that which increases the period of invasion into drone cells is minor.

3.4. Density dependent effects

The model was used to test the prediction that any *A. mellifera* or *A. cerana* colonies of a given size have a maximum theoretical mite population (Martin, 1997a). The models' predicted values for both *A. mellifera* (81000) and *A. cerana* (900) were in good agreement with the values predicted by Martin (1997a). An *A. mellifera* colony will

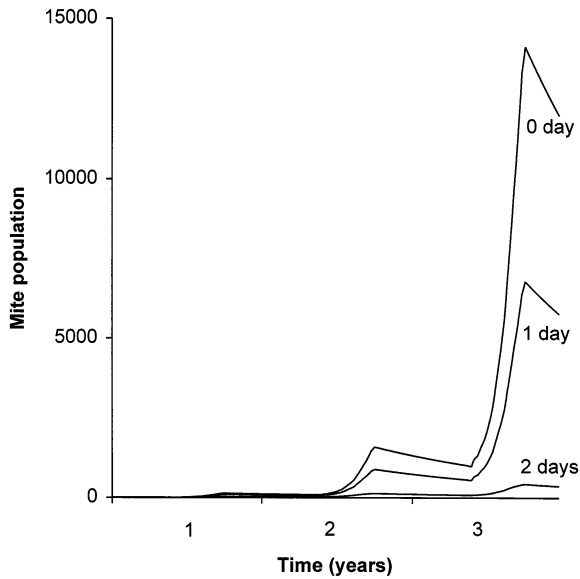


Fig. 6. Effect on mite population development of reducing the hosts' sealed developmental time by no (normal), 1 or 2 days.

collapse long before these high levels are reached, due to secondary viral infections (Martin et al., in prep). However, it demonstrates that even if mite reproduction could be restricted to

only drone brood, as in *A. cerana*, the mite population can still increase to over 10000 which is more than sufficient to cause colony collapse.

3.5. Effect of decreasing the host sealed-brood period

The idea that bees with a shorter sealed period are more resistant to the mite has been the focus of much research and bee breeding programmes. By combining the offspring mortality data (Table 3) with their developmental times (Martin, 1995b) the effect of shortening the sealed brood period on the mite population development was investigated. Fig. 6 indicates that even a 1-day reduction in the sealed brood period would only delay and not prevent the mite build-up. The model indicates that unless worker post-capping times approaching 9 days can be achieved it is unlikely that selecting bees with shorter capping times would give rise to mite-tolerant bees (Martin, 1997b). However, if shorter post-capping times are associated with increasing levels of mite mortality both within the cells and shortly after emergence (Calis et al., 1996) worker post-cap-

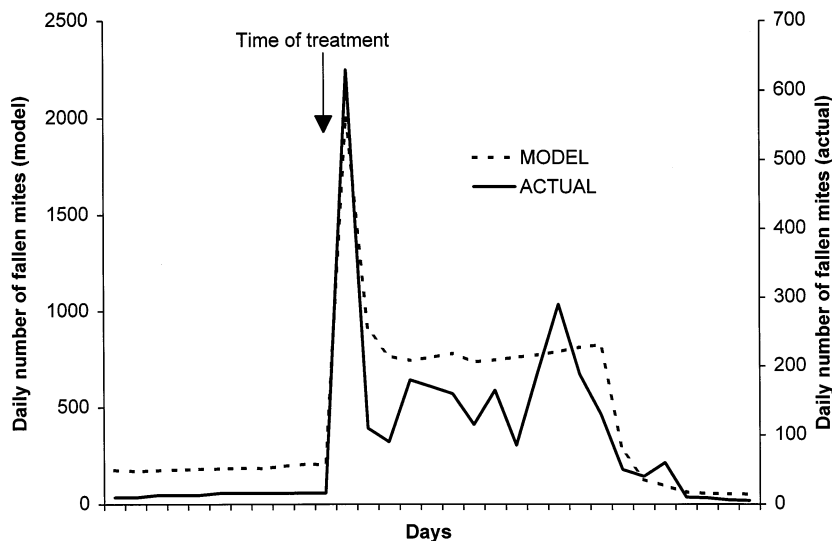


Fig. 7. Comparison of the predicted pattern of mite drop when a contact acaricide which kills 80% of the phoretic mites daily, with that recorded from an actual colony.

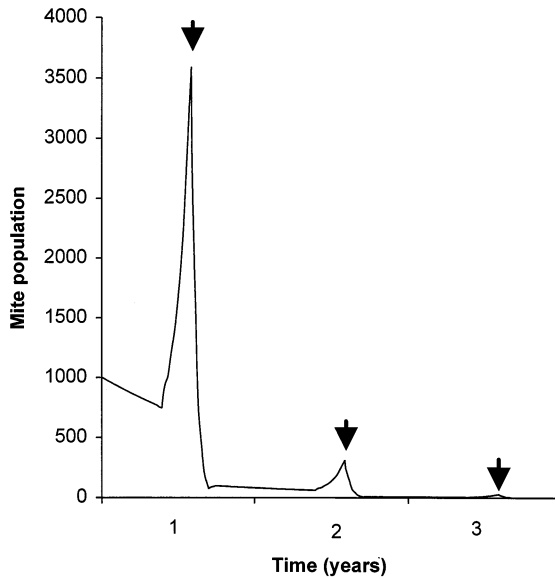


Fig. 8. Effect on predicted mite population when an acaricide treatment which is 99% effective is administered yearly (ar-row).

ping times more than 9 days may prevent mite populations increasing, but data on offspring mortality levels is needed to test this idea.

3.6. Effect of acaricide treatment

The effect of applying an acaricide was studied. When a contact acaricide with a daily efficacy of between 50 and 100% is administered, the pattern of predicted mite drop (Fig. 7) is similar to that observed in the field (B. Gant, pers. comm.). This reflects the distribution of mites within the colony and the fact that only phoretic mites are killed by the acaricide. If the overall efficacy is 99% per treatment and it is applied yearly, an initial infestation of 1000 mites is roughly halved each year (Fig. 8).

3.7. Monitoring tools

3.7.1. Daily mite drop

Recording the daily mite drop as a method of predicting the mite population is frequently used by beekeepers. However, the ratio of falling to total number of live mites in the colony is largely unknown. The model reveals that the daily ratio of live to dead (fallen) mites changes dramatically between the times brood is present and absent (Fig. 9). Altering the mites' winter phoretic, or post-

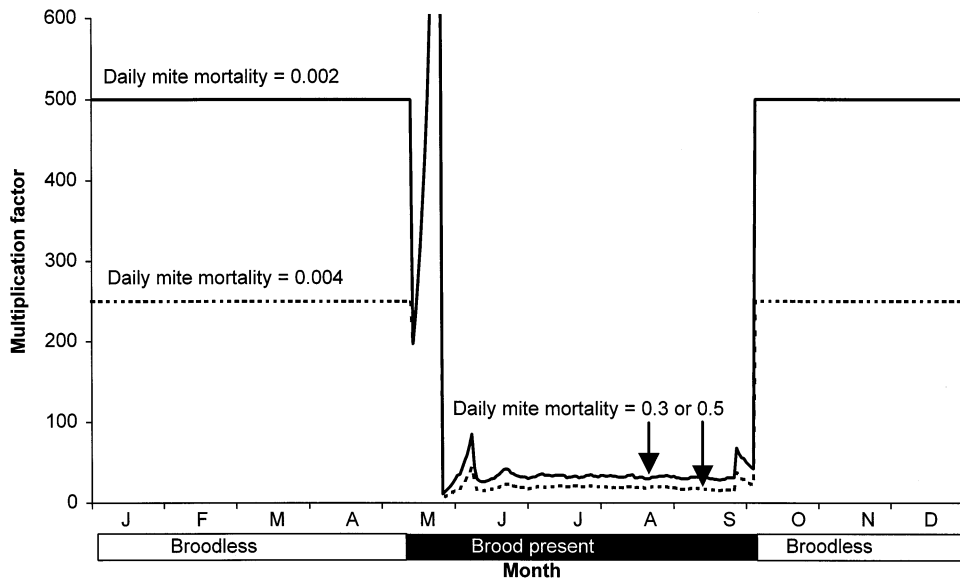


Fig. 9. Ratio of falling to total number of live mites in the colony throughout the year at two different mortality levels. The mortality levels used probably represent the edges of the range shown by these variables.

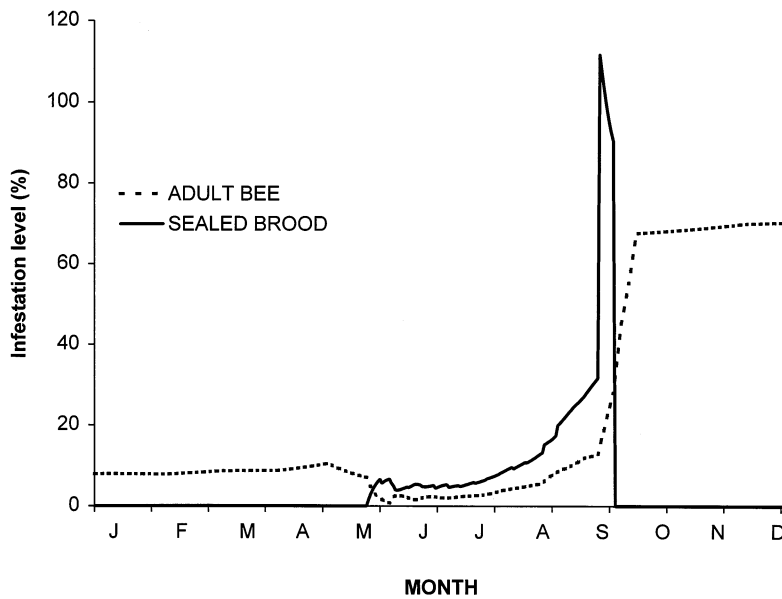


Fig. 10. Predicted infestation levels of adult bees and sealed brood during 1 year.

emergence, mortality rates affects the ratio, although the ratio is independent of the colony size, mite population and length of brood or broodless periods. So by multiplying the daily mite drop by

250–500 in the winter (broodless period) or 20–40 in the summer (brood present), a beekeeper would be able to estimate the live mite population in the colony at that time.

3.7.2. Sampling adult bees or sealed brood

By examining a small sample of bees or brood the infestation level can be quickly determined. However, since bee and brood infestation levels are determined by the stage of the colony cycle (Fig. 10) the infestation level of a sample of bees may decrease despite an increasing mite population! This is because the host population may be increasing at a greater rate than that of the mites. This means that the relationship between infestation level of brood or adult bees and the number of mites in the colony is very complex and unless good estimates of the total number of bees or brood can be determined, large errors in the predicted mite population may arise.

However, the model predicts that $\approx 65\%$ of the mite population (55% in worker and 10% in drone) are in the sealed brood at any time (Fig. 11), this can, along with the estimates of sealed brood or adult bees could be used to roughly estimate the mite population.

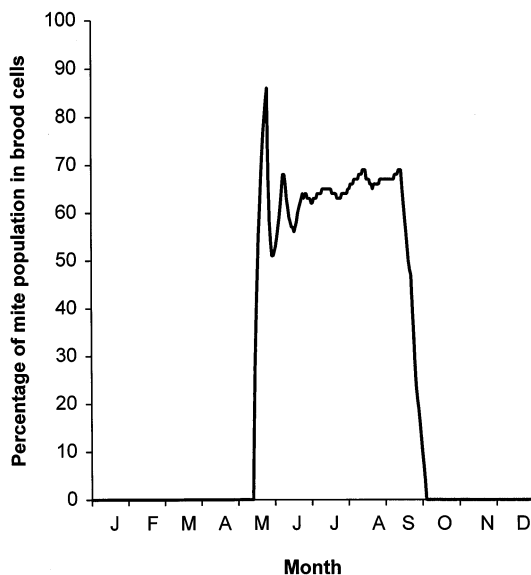


Fig. 11. Predicted percentage of the mite population within the sealed brood during the year.

4. Conclusions

The predicted mite population development corresponds well with field data. Also the values derived from the model for such behaviours as drone preference, phoretic period, etc. support the various assumptions made.

In this model there is no feedback between the mite number and host colony development, i.e. the feeding activities of the mites do not prevent the normal development of the bee colony. For beekeepers conducting effective control strategies the mite infestation level should always remain below any damage threshold and so using a similar sized colony year after year should be realistic. By using any of the monitoring methods, although very accurate bee colony data are needed if sampling of adult bees or sealed brood is used, the number of mites can be determined by the model. These data can then be used to start a model run from the day the estimate was made allowing the subsequent build up of mites to be predicted. This provides the necessary information needed so effective mite control strategies can be implemented. The model can also be used to study further the complexities of the mite–bee relationship.

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