

# Modelling Biological Approaches to Controlling Varroa Populations

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*Manuscript received for publication April 2, 2001*

## INTRODUCTION

*Varroa destructor* (Andersen 2000) is an ectoparasitic mite of the honey bee (*Apis mellifera*) which breeds in honey bee brood and if untreated, can cause colony collapse within two to three years. The eventual collapse of colonies may be due to secondary infections of viruses, but it is widely accepted that control of varroa populations prevents the collapse of honey bee colonies. There are a variety of chemical treatments available to control varroa, e.g. pyrethroid-based varroacides, but this has led to the development of resistance and many beekeepers are averse to the use of "chemical" treatments in their colonies. Therefore, there has been interest for many years in non-chemical methods of controlling varroa populations. Such non-chemical methods range from the use of biotechnical methods such as drone trapping (Calis et al. 1999), which tend to be labor intensive, to natural pheromone-based repellents or lures. A longer-term solution is to establish populations of bees, through breeding programs, which limit the build-up of varroa populations or are less severely affected by secondary pathogens associated with large mite populations.

This study used a mite population model developed by the Central Science Laboratory (CSL) to identify the changes required in European honey bee colonies to reduce the mite population growth rate. Published data were then reviewed to determine the likelihood of achieving these changes given the known levels of variations between different strains of *A. mellifera* and thus identify the approaches with the greatest potential. The aim of this paper is not to identify methods of developing varroa-resistant bees, but to identify parameters which can be changed to reduce the growth rate of mite populations to a scale where biotechnical techniques are more cost-effective and the rate of development of resistance to chemical treatments is reduced. Therefore, a goal of 25% reduction in the annual mite population growth rate has been used to determine the required changes in parameters. A change of 25% is probably large enough to warrant the use of a biological control method, and is also not unrealistically high.

The natural host of the varroa mite is the Asian honey bee *A. cerana* and it was a long-held belief that varroa infestation of *A. mellifera* colonies was simply a direct consequence of transfer from *A. cerana* colonies in mainland Asia. However, Andersen (2000) has shown that there is wide genetic variation between varroa mites infesting *A. cerana* in mainland Asia (*Varroa jacobsoni*) and those infesting *A. mellifera* in Europe, the Americas and Africa (*Varroa destructor*). Therefore, it is not a simple matter of comparing the biology of varroa in *A. cerana* colonies, where it causes minimal harm, with that in *A. mellifera* colonies and using these parameters to develop varroa-tolerant bees. However, there are some strains of *A. mellifera* which appear more tolerant to *Varroa destructor*, e.g. the Africanized honey bee *A. mellifera scutellata* in South America. Therefore, comparisons can be made between strains of *A. mellifera* to evaluate the differences in

parameters identified by the model and therefore the probability of being able to modify the parameter by the scale required to reduce the mite population growth.

## The varroa model developed at CSL

Computer models have been used previously to gain insights into the population dynamics of varroa mites (Fries et al. 1994, Martin 1998, Calis et al. 1999b, Wilkinson and Smith, in prep), and to study the importance of mite and bee parameters to mite population growth (Fries et al. 1994, Wilkinson and Smith in prep). Models have also been used to evaluate the potential value of chemical and biological control methods (Calis et al. 1999a, Calis et al. 1999b, Wilkinson and Smith, in prep). The aim here is to use modelling to specifically analyze the parameters whose values it may be possible to alter for the purpose of biological control of the mite population, for example by selective breeding.

A difference-equation model detailed by Wilkinson and Smith (in prep) was used to model a population of varroa mites reproducing in a simulated host honey bee colony. The simulated honey bee colony comprises adult worker bees, worker bee brood (eggs/larvae/pupae) and drone (male) bee brood. The colony simulation is based on a seasonal growth pattern typical of a prolific colony in a temperate country of Northern Europe, where honey bees have a main brood season lasting about six months, and a period in mid winter when virtually no brood is reared. The egg-laying rate of the queen bee is determined by a curve representing the seasonal factors such as pollen and nectar availability, and the numbers of brood cells containing drone larvae is set to a proportion of the worker bee brood. A bee mortality curve was also created to apply the higher mortality rates during summer foraging.

Simulated varroa mites either remain on adult bees (phoretic stage), or they invade brood cells to reproduce (reproductive stage). Mites were allowed to invade worker brood or drone brood according to the mite invasion rates derived by Boot et al. (1994, 1995), which include a strong preference for mites to invade drone cells. Furthermore, varroa mites produce more offspring in drone brood cells than in worker cells (Schulz 1984, Ifantidis 1984, Fuchs and Langenbach 1989, Martin 1994). Phoretic mites are subject to different mortality rates in winter and summer (Moosbeckhofer 1991, Martin and Kemp 1997, Fries et al. 1994, Korpela et al. 1992, Boot et al. 1995, Calis et al. 1999b), and mites emerging from the brood cells (as the young bee emerges) are also subject to emergent mortality (Boot et al. 1995, Lobb and Martin 1997, Martin and Kemp 1997). For simplicity, and following previous models, we assume that varroa mites do not affect the population dynamics of the bee colony.

The model was seeded with 10 female varroa mites, and the daily mite population recorded throughout each simulation. Each simulation modelled a one-year period. Elasticity-type sensitivity analysis was performed: each of a range of honey bee and varroa mite parameters was varied in turn to determine the percentage

change needed to bring about a 25% reduction in the annual growth rate of the mite population.

Since the model is intentionally kept simple to avoid problems of over-parameterization, the effects of some parameter changes were modelled indirectly. For example, changes in cell size could reduce the invasion rate or the average number of viable daughters produced per mother. Some factors might be adjustable in respect of just drone cells, or just worker cells, so the effects were modelled for each in turn, and then also in combination. The results of the sensitivity analysis are summarized in Table 1.

### Investigating methods of controlling varroa

When considering factors in bee biology that can be used to control varroa populations, it is obviously important to consider the heritability of the trait, together with any associated adverse effects on the viability of the colony. However the aim of this study is simply to identify the parameters which could be investigated further. The heritability of some traits which may be useful in controlling varroa populations is reviewed in detail by Harbo and Harris (1999). The parameters identified by the model were reviewed to determine the scale of variation reported in European honey bee colonies and in Africanized honey bees which have been reported to be more tolerant to *Varroa destructor*. These data were then compared with the changes identified by the model as the minimum required to reduce the mite population growth rate by 25%. The results were then collated to produce a shortlist of parameters in European honey bee colonies which could be used to limit the growth of mite populations.

### Altering the proportion of drone brood

The importance of drone brood in determining the mite population growth rate has been shown by Wilkinson and Smith (in prep). The model predicted that to reduce the mite population growth rate by 25% requires a 19% reduction in the proportion of drone brood (Table 1). The 19% reduction in drone brood amount equates to a reduction from 4% to 3.2% drone brood for the honey bee colony developed in the model.

**Table 1. The size of the parameter adjustments required to produce a 25% reduction in end-of-year mite population.**

Parameter	Original value in the model	Percent Change Required
Invasion Rate [drone Cells]	Dynamic*	-19
Invasion Rate [worker Cells]	Dynamic*	-96
Invasion Rate [drone and worker Cells]	Dynamic*	-16
Viable Reproduction Rate [drone Cells]	2.44	-12
Viable Reproduction Rate [worker Cells]	1.06	-9
Viable Reproduction Rate [drone and worker Cells]		-5
Emergent Mortality Rate [drone Cells]	0.17	+41
Emergent Mortality Rate [worker Cells]	0.30	+10
Emergent Mortality Rate [drone and worker Cells]		+8
Phoretic Mortality (winter)	0.003	+50
Phoretic Mortality (summer)	0.016	+61
Phoretic Mortality (winter & summer)		+27
Proportion Drone brood	0.04	-19
Post-capping time [drone Cells]	288 hrs.	-9 (equivalent to -30 hrs)
Post-capping time [worker Cells]	336 hrs.	-7 (equivalent to -20 hrs)
Post-capping time [drone and worker Cells]		-7

\* The invasion rates derived by Boot et al. (1994) and Boot et al. (1995) are dependent on various parameters, and vary through the season.

The defensive nature of the Africanized bees, where varroa is not a significant problem, means that exact and regular assessments of honey bee population dynamics are rare including the ratios of worker to drone brood, seasonal patterns of swarming and

brood rearing which could limit the build-up of varroa populations (Rosenkranz 1999). There is also little robust data available on the levels of drone brood produced by different strains of honey bee in a range of climatic and nectar flow conditions representative of the normal habitats of the European honey bee. Generating these data would be the first step in selecting strains of bee producing low levels of drone brood. However, in the absence of bees which naturally produce lower levels of drone brood, control of drone brood levels by the beekeeper offers a significant interim control measure. The attraction of mites to drone brood is widely used in biotechnical control methods (Calis et al. 1999).

### Altering the invasion rate of brood cells by the mite

The model suggests that the invasion rate of worker cells would need to be decreased by 96% to reduce the mite population growth rate by 25% (Table 1). Such a large reduction is necessary because mites which do not enter worker cells are available to invade drone cells. Since mite reproduction is greater in drone cells, only a proportion of these "displaced" mites need to enter drone cells to balance the loss of population growth. The attractiveness of the brood to varroa mites may be affected by a number of factors which may interact, including the size of the cell and the strength of the pheromone signal.

### The size and shape of the brood cells

The diameter of the worker cell appears to affect the invasion of varroa mites. In the absence of drone brood, the varroa infestation rate has been reported to be 16-50% lower in the small Africanized worker cells than in the larger European (Italian) worker cells (Guzman-Novoa et al. 1999, Rosenkranz 1999). This in part may have been due to a higher visitation rate by nurse bees as the European larvae were larger and heavier, and to the longer periods spent capping the larger cells which would increase the time period over which a mite can invade the cell (Message and Goncalves 1995).

Drone cells containing worker brood were less attractive to mites than worker cells containing worker brood, whereas drone larvae in worker cells were attractive for a longer period than those in drone cells (Beetsma et al. 1999). This suggests that varroa invades the cell when the larva fills the cell-bottom. In plastic cells which have a slightly larger diameter, the time the worker larvae are vulnerable to invasion is reduced from 14 hours to six hours, i.e. by 58% (de Jong 1997). Making worker cells slightly larger might reduce attractiveness, but by far less than the 96% change identified by the model.

The depth of cells also affects invasion rate: invasion begins when the larva is between 7 to 7.5 mm from the comb surface and increases exponentially until the cell is sealed (de Jong 1997). Elongated worker brood cells were attractive for a shorter period than normal worker cells and contained only 16-50% of the mites (Beetsma et al. 1999). Shortened worker cells contained 200-300% more mites than normal worker cells. However this approach does not achieve the 96% reduction required and is impractical in modern honey bee colonies.

Drone brood cells are susceptible to invasion 2 to 3 times longer than worker brood (40-50hrs compared to 15-20hrs) (Beetsma et al. 1999). Although mites which do not invade drone brood are available to enter worker cells, their reproductive growth is less. Thus only a 19% reduction in drone cell invasion is required to reduce the annual mite population growth rate by 25%. This suggests that reduction of the window for invasion by the 19% required offers a possible route to limiting mite population growth. This might be achieved by increasing the diameter of the drone brood cells slightly to reduce the length of the window for invasion between the larva filling the bottom of the cell and capping. If similar to the effect reported for worker brood, this would reduce the invasion rate by 58% which is far more than the 19% required. Realistically, breeding bees which produce larger cells for drone laying but not larger drones is unlikely. An alternative

approach would be introduction of artificial comb with slightly larger cells but the proportion provided would need to be carefully controlled, so as not to encourage mite breeding.

### Strength of chemical signals

Trouiller and Milani (1999) reported that the chemical signals produced by bee larvae attracts varroa into the brood. This offers the potential to modify the signal and reduce attractiveness of the brood. No differences in larval attraction between Africanized and European worker brood have been reported in laboratory or colony trials (Rosenkranz 1999, Beetsma et al. 1999) suggesting that there are no, or only slight differences between strains of *A. mellifera*. However there are differences between castes. The preference of mites for drone brood is probably due to the signal(s) the mite receives from a brood cell in its direct vicinity (Beetsma et al. 1999). The larger drone larvae produce higher levels of kairomones, including esters such as methyl palmitate which has been shown to be highly attractive to varroa (Le Conte et al. 1989, Rosenkranz and Engels 1985). Queen cells are rarely reported as invaded, which may be related to a weaker attractive signal. Trouiller et al. (1994, 1992) showed that queen larvae produce low levels of methyl palmitate, methyl linoleate and ethyl palmitate, which are mite attractants and produce higher levels of methyl oleate, a mite repellent. Queen cells have a short post-capping time (8 days) and it would be a reproductive disadvantage for mites to invade queen cells.

To achieve a 25% reduction in the mite population, the attractiveness of the drone brood would need to be reduced by 19%, the worker brood by 96% or a combined reduction of just 16% (Table 1). It is likely that a 96% reduction in worker brood pheromones would significantly affect the colony. The brood produces pheromone(s) that inhibit worker ovary development and egg laying (Winston and Slessor 1998), as well as a secondary signal that inhibits queen rearing.

The more realistic approach would require selecting for bees that produce drone brood which is at least 19% less attractive to the mite. The high levels of semiochemicals produced by drone brood offer the opportunity to alter the balance of attractant and repellent chemicals using breeding programs, but it is unclear at this stage what level of reduction would be achievable or the impact on the colony.

The phoretic period is simply the reciprocal of the invasion rate. It appears that mites need to feed on adult bees prior to cell invasion, so as to advance development of the mother mites and allow an earlier start to oviposition (Beetsma et al. 1999, de Jong 1997). The requirement for this is currently unclear, but if there is a minimum requirement for the phoretic period, e.g. 1 day, a 16% increase, i.e. 3.8hrs, would be sufficient to limit the growth of the mite population by 25%. Before being pursued further, this approach requires further data to confirm the mite's requirement of a minimum phoretic period.

### Altering the viable reproduction rate of the mite

Oocytes in the female mite are in the previtellogenic phase when she enters the larval cell. Embryogenesis only starts after the cell has been capped and only if the mite has come into contact with a 5 day old larva within 24 hrs after capping (Trouiller and Milani 1999). The first egg is then laid 60-70hrs after capping. The male mite hatches first and each of the subsequent female mites mate soon after hatching. The number of reproductive cycles (i.e. the number of times a mite enters cells to reproduce) which a female mite can perform in the laboratory is as high as seven (de Jong 1997), but closer to 2-3 in manipulated colonies (Martin and Kemp 1997, de Jong 1997). This variation is probably due to variability between female mite offspring in the success of mating (Donze and Guerin 1994).

The viable reproduction rate depends on the fertility of the mother mite when the cell is capped over, and is determined by the production of a male offspring, the number of daughters produced by the mother mite, and the number of the daughter mites which

mate successfully. The viable reproduction rate also depends on the post-capping time.

### Mite fertility

Several workers (Message and Goncalves 1995, Guzman-Novoa et al. 1999, Ruttner, et al. 1984, Rosenkranz 1999, Medina and Martin 1999) showed low rates of mite fertility: 40-50% in worker brood of Africanized and European bees in Brazil and Mexico. In these studies female mites entered worker cells but did not lay eggs. However, this effect was worker brood specific as about 90% of mites entering drone cells of Africanized bees were fertile (de Jong 1997). Significantly higher (69%) mite fertility was reported in worker brood of hybrids between European and Africanized bees in Mexico (Guzman-Novoa et al. 1999). The stability of mite infertility in Africanized bees in Brazil, the breakdown when mites were transferred to European bees, and the high fertility in drone brood suggests that it is a host rather than a parasite trait (Rosenkranz 1999).

Mite fertility in European races of honey bees in more temperate climates appears to be higher than those in Africanized or European bees in Mexico and Brazil, with reported values ranging from 60% to 90% (Rosenkranz and Engels 1994, Garrido et al. 2000, Harbo and Harris 1999, Rosenkranz 1999). In European bee colonies with high levels of non-reproducing mites, those mites that did reproduce produced fewer progeny suggesting decreased reproduction was due to absolute infertility, reduced fecundity and higher mite mortality in brood cells (Rosenkranz 1999, Medina and Martin 1999). Differences in mite fertility could, at least in part, be explained by differences in semiochemicals between bee species, races, strains, sexes or castes, as well as the reaction of different mite genotypes towards these signals (Trouiller and Milani 1999). It is therefore important to identify what triggers egg-laying in female mites if it is to be suppressed.

The model suggests that the viable reproduction rate in drone and worker brood would need to be reduced by 5-12% to decrease the mite population growth rate by 25% (Table 1). The fertility of mites from worker brood varies widely between bee strains and suggests that breeding programs may result in traits which reduce mite fertility. To reduce the mite population by 25% requires only a 9% reduction in the viable reproduction rate in worker cells. The 90% fertility in Africanized drone cells is similar to that in European drone cells (de Jong 1997) suggesting that there is less opportunity to affect the viable reproduction rate in drone cells through breeding programmes.

Selective breeding of *A. mellifera* queens that could suppress mite reproduction has been reported (Harris and Harbo 2000). They identified a delayed suppression of mite reproduction which is a heritable characteristic. The reproduction of mites was unchanged in the first brood cycle, but the mean number of progeny produced by mites in worker brood was reduced by more than 50% after 5 to 6 weeks. They considered the most likely explanation for the reduction in mite fertility was that the brood affected mite fertility. Up to 75% of the mites could not lay eggs, with an increased number, up to 27%, of mites dying in the cells trapped by the cocoon. This compared with 10-15% of mites unable to lay eggs, and 1-2% dying in cells, in susceptible honey bee strains. They suggested that these effects were due to poor mating events in brood cells as they reported greatly reduced sperm counts in live mites that did not lay eggs. This decrease in mite fertility from 85% to 25% is well in excess of the 9% reduction required to decrease the mite population growth rate by 25%. No data were reported for the reproduction of the mite in drone brood.

### Shortening the post-capping time

Shortening the post-capping time reduces the number of offspring that can be produced and the time for the last offspring to successfully mate prior to emergence. Post-capping periods for worker European bees have been reported to vary from 268 to 290 hrs (Harris and Harbo 2000) and the model is based on a post-capping period of 288 hrs for workers and 336 hrs for drone brood.

Worker Africanized bees usually have a post-capping period 20 hrs shorter than European bees (Rosenkranz 1999). However, among European bees there is significant variation in the average duration of the capped period and this is a heritable characteristic (Harris and Harbo 2000), but it can be affected by climatic conditions. European *Apis mellifera carnica* bees had a worker post-capping time only 8 hrs longer than Africanized bees at the same tropical site (Rosenkranz 1999).

The model predicts that, in order to bring about a 25% reduction in mite population growth (excluding the possible effects of reduced mating success and fertility of daughter mites) the post-capping period for worker brood needs to be reduced by 7% (20 hrs) for worker brood, by 9% (30 hrs) for drone brood and by 7% (20hrs worker, 24hrs drone) for both. This results in a post-capping time close to the minimum reported for worker brood, but drone brood has greater phenotypic variation (de Jong 1997) suggesting that it may be possible to breed bees that produce drone brood with a shorter post-capping period. Buchler and Drescher (1990) reported that 25% of the variation in mite populations in their colonies could be accounted for by variations in the post-capping period, which fits in well with the results of our model. However, in a survey of European bees an average 8.7% reduction of mite infestation rate was calculated for each 1hour reduction in the capping time (de Jong 1997). This is a much larger effect than our model predicts, suggesting other factors are confounding the comparison in European bees.

### Emergent mortality

The emergent mortality represents the death of mites at the time of the host bee emerging, or soon after. It also represents the death of mites in cells opened early, for example due to hygienic behavior. Hygienic behavior is where the bees (a) detect and uncapped infested cells, and (b) remove the dead or diseased larvae and pupae, together with the mother and daughter mites. The mites do not leave the cells until most of the body of the larva or pupa have been removed by the bees (Boecking and Spivak 1999). The death of immature mites results in a reduced viable reproduction rate. The hygienic behavior of bees therefore offers the ability to both reduce the viable reproduction rate and increase mite mortality.

Africanized bees have been reported to remove up to 32% of

infested brood (Guzman-Novoa et al. 1999, Rosenkranz 1999) compared with 8-17% in European strains (Boecking and Spivak 1999). However, *A mellifera ligustica* bees pre-selected for hygienic behavior removed an average of 52% of infested pupae (Boecking and Spivak 1999). A higher proportion of brood containing 2 mites was removed, than was brood containing a single mite (de Jong 1997).

Spivak (1996) has reported that hygienic behavior is a heritable mechanism of resistance to varroa in *A. mellifera* and colonies selected for hygienic behavior had lower mite levels than non-hygienic ones in some experiments. The hygienic behavior can be increased from a maximum of 17% to 52% by a selective breeding program (Boecking and Spivak 1999). Of the mites removed, 61.3% have been shown to invade new brood cells, 14.6% became phoretic and 24.6% were either killed by bees or found on the hive floor (Boecking and Spivak 1999). Thus, hygienic behavior would increase mature female mite mortality by 9% compared to non-hygienic bees, and reduce the reproduction rate and the number of reproductive cycles for those adult mites that did survive. Therefore, when compared with the model predictions on the basis of the emergent mortality alone, hygienic behavior can make a significant contribution to controlling mite populations if applied to both worker and drone brood (8% reduction required), but is insufficient when applied to worker (10% required) or drone brood (41% required) alone. In addition, hygienic behavior would reduce the average reproduction rate, and assuming an additive effect, this would be sufficient to limit the growth of the mite population. In practice, results are likely to be highly variable as the level of hygienic behavior is reported to depend on the level of pollen storage, colony strength and nectar flow (Boecking and Spivak 1999, Janmaat and Winston 2000).

### Changing the phoretic mortality rate

There are a number of factors which can be used to alter the phoretic mortality of varroa mites, apart from the rapidly effective acaricides which are used to treat colonies. Honey bees are able to kill and injure mites during their phoretic period and fallen mites can be observed to have damaged legs and dorsal shield. There are widely varying data reported on the effectiveness of grooming in the removal of varroa mites. Italian strains have been reported to

**Table 2: Possible changes in honey bee colonies identified as having the potential to produce the required changes in the model parameters to reduce the mite population growth rate by 25%.**

Parameter	% changes required	Changes possible	Short term measures	Longer term prospects
Proportion drone brood	Minimum -19%	Levels of drone brood not clear, decrease from 4% to 3.2%?	Physically control proportion drone brood	Breed bees with lower drone brood production
Invasion rate	-16% (drone and worker) to -96% (worker)	Drone cells size and semiochemicals to reduce attractiveness by 58%? Length phoretic period?	Introduce larger celled drone comb	Breed bees with drone which produce lower levels of semiochemicals
Viable reproduction rate	-5% (drone and worker) to -12% (worker)	Reduce mite fertility by 30-60%	Some progress in breeding bees which suppress mite fertility	Identify semiochemicals that trigger egg laying and develop method to suppress
Emergent mortality rate	+8% (drone and worker) to +41% (drone)	Increase hygienic behavior from 17% to 52%, Increase emergent mortality by 9%, plus effects on viable reproduction rate	Selection of bees with greater hygienic behavior	Identify mechanism to reduce successful mating of female mites and therefore number of reproductive cycles
Post-capping time	-7% (drone and worker) to -9% (drone)	Maximum 7% worker, unknown for drone will also affect viable reproduction rate	None	Select for bees with shorter drone capping times
Phoretic mortality	+27% (all year) to +61% (summer)	Unknown	None	Select for nurse bees with lower attraction for mites

be only 14% as efficient as Africanized bees at removing mites from their bodies (Guzman-Novoa et al. 1999, Rosenkranz 1999) and mites that are removed may still be capable of reproducing (Rosenkranz 1999). In *A. cerana* 30-99% of introduced mites have been observed to be visibly damaged, whereas 0.03-48% were damaged in *A. mellifera* colonies (Peng et al. 1987, Buchler et al. 1992, Fries et al. 1996, Boecking and Spivak 1999). Some of these variations were due to the type of data collected, e.g. movement of mites to other bees or total removal from the colony. Murihas (1999) reported grooming efficiency of bees removing phoretic varroa mites as 0.1-0.16% in *A. mellifera* strains, suggesting very little if any of the currently reported resistance to varroa can be associated with grooming behavior.

An alternative approach is to alter the attraction of the mites to nurse bees which transport them to suitable brood. Mites are strongly attracted to nurse bees rather than foragers as foragers produce higher levels of alarm pheromone and Nasanov pheromone which repel varroa (de Jong 1997). Therefore, if the attractiveness of nurse bees could be reduced or that of the foragers increased, the invasion rate of the brood would be altered as a lower proportion of the mites would reside on nurse bees visiting brood. Also phoretic mortality may increase as the mites are transported outside the colony on foragers, and some of the bees with mites die away from the hive.

The model suggests that the summer mortality would need to be increased by 61% or the winter mortality rate by 50% to reduce the mite population growth rate by 25% (Table 1). The summer daily mortality rate would therefore need to increase from 0.016 to 0.026 and the winter daily mortality rate from 0.003 to 0.005. This shows that grooming, which would be the only method of affecting winter phoretic mortality, cannot be seen to contribute to increasing the winter or summer mortality rate significantly. Lowering the preference of the varroa mites for nurse bees by altering the pheromone levels in foragers may alter the summer phoretic mortality rate significantly, but is a long-term prospect.

## CONCLUSIONS

There has been increasing interest in breeding varroa-tolerant bees over the last years, especially as varroa mites develop resistance to acaricides. This review has shown that it important to understand the factors which can affect the build-up of the mite population within the colony. The changes required and the progress in achieving them to date are shown in Table 2.

In almost all cases using the factors identified, the build-up will be delayed rather than prevented, but this would allow biotechnical methods to be more cost-effective and the development of resistance to varroacides to be delayed. There has been progress in the development of apparently varroa-tolerant strains, although care must be taken to define the species and haplotype of varroa under investigation. Progress has been made in the development of strains which appear to suppress mite reproduction directly (Harris and Harbo 2000), through reduced brood development time (de Jong 1997) and through increased hygienic behavior (Boecking and Spivak 1999). The model has highlighted a number of other approaches and allowed us to quantify the level of change required to affect the mite population growth rate, and to determine whether they are achievable. These approaches have been evaluated in isolation, but in practice there are likely to be more than additive effects if more than one parameter is affected, e.g. by increasing hygienic behavior. This review has concentrated on highlighting possible approaches. What it has not considered is the stability of the heritable traits, particularly with outcrossing of queens with drones from less resistant stock, and the influence on the colony viability and productivity of selecting for these traits.

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