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Dynamics of the parasitic (*Varroa jacobsoni*) population: Modelling criteria

I. FRIES

ENTOMOLOGY DEPARTMENT

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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SWEDEN

SUMMARY - The basic structure of the *Varroa* mite and honey bee relationship is described to allow the construction of a mathematical model of the mite population dynamics. Necessary criteria for building the model is commented. In the mite reproduction part of the model, the demand of relevant bee brood data and the understanding of variations in mite fertility, especially on worker brood, are emphasized. In the mite mortality part of the model, it is pointed out that there is a lack of information on the proportion of mites that die but that do not end up in the hive debris. In cold climates, the loss of mites, as bees die during winter is important to limit the mite population growth. In regions with extended brood rearing, mite mortality data during flying conditions is vital. The presented model does not include the effect of mites on bee population dynamics. Thus, it is only relevant for infestation levels below a certain threshold. Such a model may still be used for simulating effects of control treatments or breeding programmes for mite tolerance. Simulations indicate that the proportion of infertile mites in the worker brood is a key factor for limiting mite population growth.

Key words: *Varroa jacobsoni*, honey bees, population dynamics, computer modelling.

RESUME - "La dynamique des populations du parasite *Varroa jacobsoni* : Critères de modélisation". La structure fondamentale du rapport entre l'acarien *Varroa* et l'abeille mellifère est décrite afin de permettre la construction d'un modèle mathématique concernant la dynamique des populations de l'acarien. Les critères nécessaires pour la construction du modèle sont commentés ci-après. Dans la partie du modèle qui concerne la reproduction de l'acarien, il est souligné le besoin d'information pertinente sur le couvain de l'abeille, particulièrement celui d'ouvrière, pour comprendre les variations de fertilité chez l'acarien. Dans la partie du modèle qui concerne la mortalité de l'acarien, il faut signaler qu'il y a un manque d'information sur la proportion d'acariens qui meurent dans la ruche mais qu'on ne retrouve pas dans les débris de la ruche. Dans les climats froids, la réduction du nombre d'acariens liée à la mortalité hivernale des abeilles, est un fait assez important pour limiter la croissance des populations d'acariens. Dans les régions ayant une longue période d'élevage de couvain, les données sur la mortalité de l'acarien pendant la période de vol de l'abeille, sont vitales. Le modèle présenté n'intègre pas l'effet des acariens sur la dynamique de la population d'abeilles. Par conséquent, il n'est applicable que pour les niveaux d'infestation en dessous d'un certain seuil. Ce modèle peut également être utilisé pour simuler les effets d'un traitement de contrôle ou l'efficacité de programmes d'amélioration de la tolérance aux acariens. Les simulations indiquent que la proportion d'acariens non fertiles par rapport au couvain d'ouvrières est un facteur essentiel pour limiter la croissance des populations d'acariens.

Mots-clés : *Varroa jacobsoni*, abeille mellifère, dynamique des populations, modélisation mathématique.

Background

The ectoparasitic mite *Varroa jacobsoni* has become the most serious pest for the European honey bee *Apis mellifera* on a world-wide scale. In most cases, the infested

honey bee colonies will die if the mite population is not controlled (Ritter, 1981). Although colony collapse is closely related to the mite population build-up, the direct causes for colony deaths seem to be secondary virus infections. The feeding of the mite activates virus replication (Acute Bee Paralysis Virus, APV, and possibly others) in infested bees and the mite then acts as a vector for these virus particles transmitting them both to adult bees and pupae (Ball and Allen, 1988). However, the original host for this parasite, the Asian honey bee *A. cerana*, is not severely damaged by the parasite.

Over the last decades, considerable insights in the *Varroa* mite biology in the Western honey bee have accumulated and quantitative data now exist for most important aspects of mite population dynamics. However, we still lack fundamental understanding of how the natural host-parasite relationship exhibited in *A. cerana* is made up. Although several traits leading to mite resistance in the Asian honey bee have been described (Peng *et al.*, 1987), we still have not been able to evaluate the relative importance, for mite resistance in *A. cerana*, of grooming behaviour, reproduction on drones only, or any other possible combination of mechanisms (Fries *et al.*, 1996).

Mathematical modelling offers a powerful tool to investigate complicated systems, among them, biological events. Provided that the construction of the model is relevant and that the actual data that goes into the model are accurate, much understanding of how the system is made up and reacts can be gained by comparing the impact of changes in parameter values. However, very few attempts have been made, however, to compile current knowledge of *Varroa* mite interaction with the honey bee into a useful mathematical model of the parasite's population dynamics. Specific aspects of the mite population growth have been modelled by various authors (Schulz, 1984; Omholt and Crailsheim, 1991; Fuchs and Langenbach, 1989; Camazine, 1988; Boot *et al.*, 1994; Boot *et al.*, 1995b) but only Fries *et al.* (1994) have presented details of a comprehensive model describing the factors affecting the population growth of *V. jacobsoni*. Based on an extension of this work (Fries *et al.*, 1994), important criteria for developing a functioning model of the *Varroa* mite population dynamics are discussed. Limitations of the model are emphasized and examples of how a workable model may be used are given.

The model structure

The basic structure of the *Varroa* life cycle in honey bee colonies is very simple. The mites sit on the adult bees (phoretic mites) where they are able to survive for extended periods feeding on the bee haemolymph. From the adult bees, some mites are lost from the system due to mite mortality. Mite reproduction can only occur when brood is available. In the brood cells, reproduction occurs, but also some mite mortality. As the bees emerge from the cells the surviving mother mites along with their adult female progeny return to the stage as phoretic mites. In simple terms, the basic feature of this model is one of exponential growth as brood is available and of exponential decay as no brood is available. The problem for most colonies of the Western honey bee is that over an extended period, the mortality factors do not balance the growth factors to an equilibrium. In Fig. 1 the basic structure of the mite life cycle is outlined.

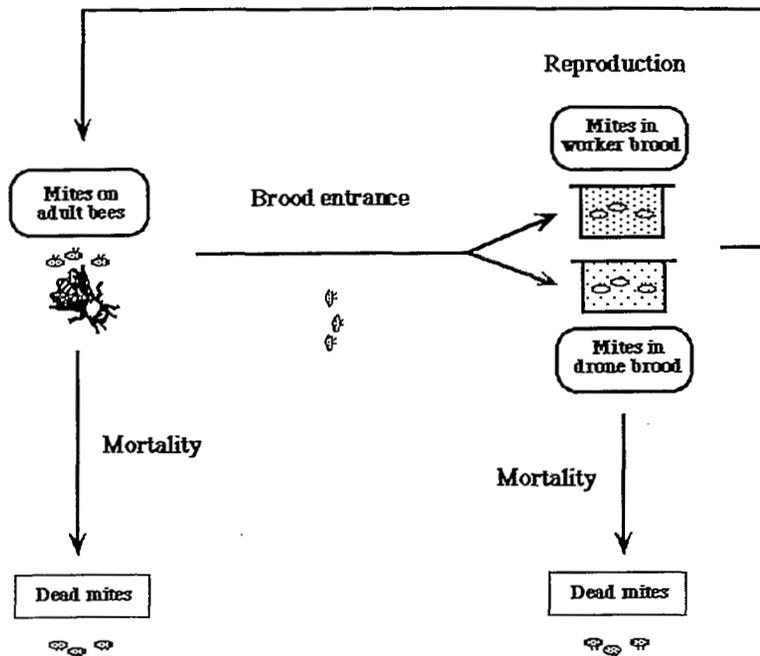


Fig. 1. Simple schematic flow chart of the *Varroa* mite population dynamics.

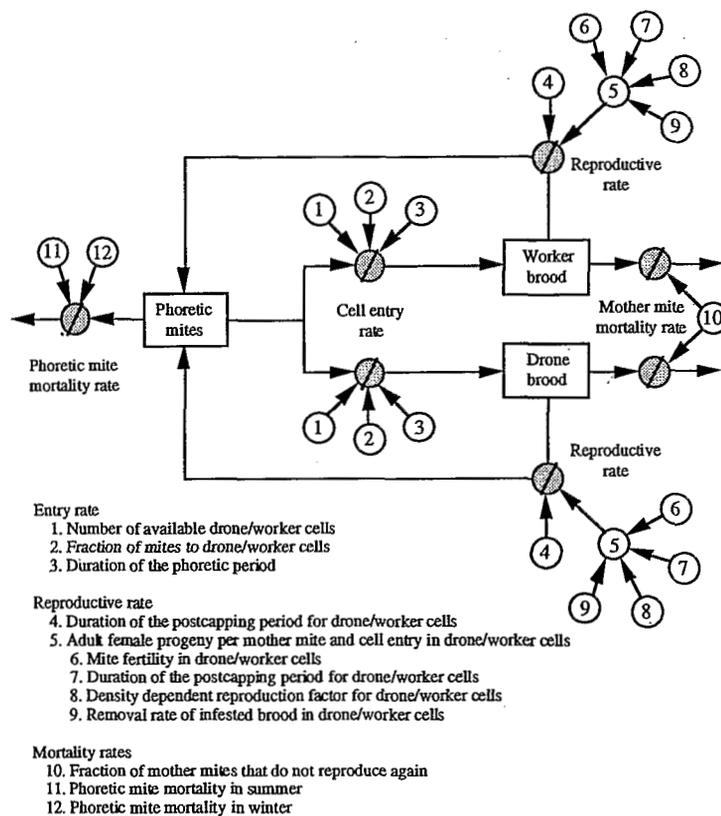


Fig. 2. Diagram of *V. jacobsoni* population growth within a honey bee colony. Three processes (described as rates) are depicted: (i) phoretic phase during which mites enter the brood cells; (ii) a reproductive phase in the brood cells; and (iii) mortality. The major factors that influence each rate are listed in the graph. Emigration and immigration of mites from/to other colonies are not included. Reproduced with permission from IBRA, Bee World (Fries *et al.*, 1994).

When various aspects of the mite and bee biology are integrated into the model, the system becomes more complex, although the basic structure still is the same. In Fig. 2, a number of relevant factors that influence the rates at which mites reproduce and die have been superimposed on the more simple structure in Fig. 1. For a discussion of parameter values used in the model the reader is referred to Fries *et al.* (1994).

Criteria for modelling

In accordance with Fig. 1, the most important criteria that affect the *Varroa* population dynamics are listed in Table 1. The Table is an amended version from Fries *et al.* (1994). One adjustment is the removal of the factor "Number of reproductive cycles of mother mites" under the heading "Reproduction". This improvement has been made possible since more accurate mortality data have become available (Calatayud and Verdú, 1994; Boot *et al.*, 1995a; Calatayud and Verdú, 1995), thus yielding a model without forcing a specified number of reproductive cycles on the mite.

Table 1. Major factors affecting the population dynamics of *Varroa jacobsoni*

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- | | |
|--|--|
| 1) Reproduction | <ul style="list-style-type: none"> - Number of female offspring per mother mite <ul style="list-style-type: none"> Reproduction in worker versus drone cells Postcapping period of drone and worker brood Density dependent reproduction <ul style="list-style-type: none"> Number of mites entering brood Number of available brood cells <ul style="list-style-type: none"> Attractive period of worker and drone brood Honey bee brood rearing dynamics - Fertility of female mites - Removal of infested brood by worker bees |
| 2) Movement of female mites into cells | <ul style="list-style-type: none"> - The bee/brood ratio <ul style="list-style-type: none"> Brood availability Removal of infested brood by worker bees - Brood attractiveness - Mite preference for drone versus worker brood - Number of mites on adult bees |
| 3) Mortality | <ul style="list-style-type: none"> - Mortality on adult bees - Mortality within brood cells <ul style="list-style-type: none"> Removal of infested brood by worker bees |
-

Another improvement of the earlier model is the inclusion of equations for mites moving into worker brood and drone brood based on the bee/brood ratio (Boot *et al.*, 1994; Boot *et al.*, 1995b). The use of an average "Phoretic period" for female mites may still yield similar over-all results, but the advantage of using a dynamic bee/brood

relationship to describe the movement of mites into brood cells becomes obvious when we consider low brood numbers. Then the probability of mites actually finding suitable cells will be reduced, which was not accounted for in earlier versions of the model.

A sensitivity analysis of the present model demonstrates that some of the criteria that deal with mite reproduction are crucial for the population build-up of the mite. It is obvious that it is imperative for the mite to have access to worker brood to cause a population build-up that eventually will cause damage to infested colonies (Fig. 3). This is congruent with the situation in the original host, *A. cerana*, where reproduction occurs in drone brood only (Koeniger *et al.*, 1981). The high preference for drone brood in *A. mellifera* (Fuchs, 1990) could indicate that the mite may develop into a drone parasite in the Western honey bee as well as if natural selection was permitted.

It is also obvious from simulation studies that the fertility of female mites on worker brood is crucial to mite population build up (Figs 4 and 5). Again, this is congruent with the situation in *A. cerana*, where the fertility is 0 on worker brood, but also in Africanized bees in Brazil. In these bees the mites do not build up detrimental population levels at least partly because of the limited mite fertility on worker brood (Camazine, 1986; Rosenkranz and Engels, 1994). Recent data from Mexico, however, indicate that Africanized bees may be tolerant to mite infestations in spite of good reproductive success in worker brood (Guzman-Novoa *et al.*, 1996).

From studies in Germany, we know that the fertility of female mites on worker brood shows seasonal variation (Otten and Fuchs, 1990). The impact from a reduced mite fertility during early spring and late autumn is not so large in a population dynamics model dealing with long winter conditions, due to the overall explosive bee population development and the low brood numbers during these periods. Under conditions with more extended brood production it may be more important to know and include the mite fertility changes on worker brood throughout the year. In any case, mite fertility in worker brood is a key factor for understanding the growth of the mite population and small changes in this parameter has a large impact on the population growth.

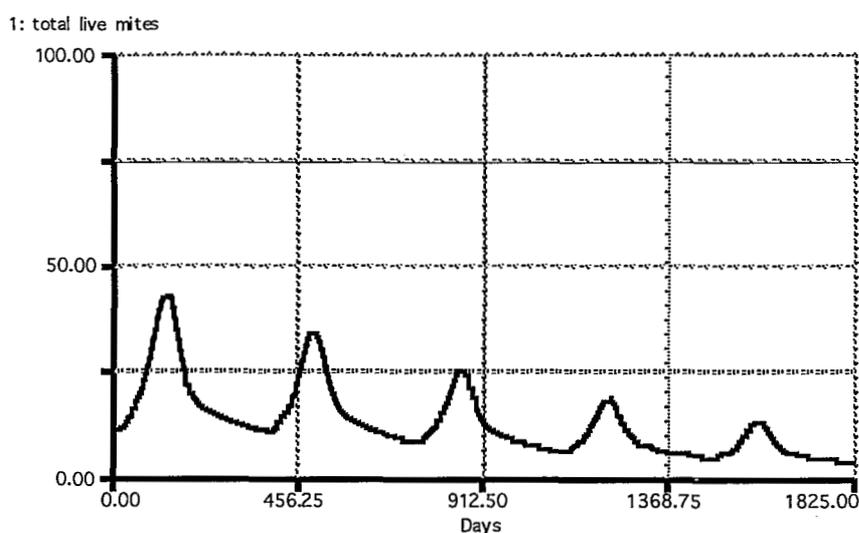


Fig. 3. Simulation of *Varroa* population development without reproduction in worker brood (Background data from Friès *et al.*, 1994).

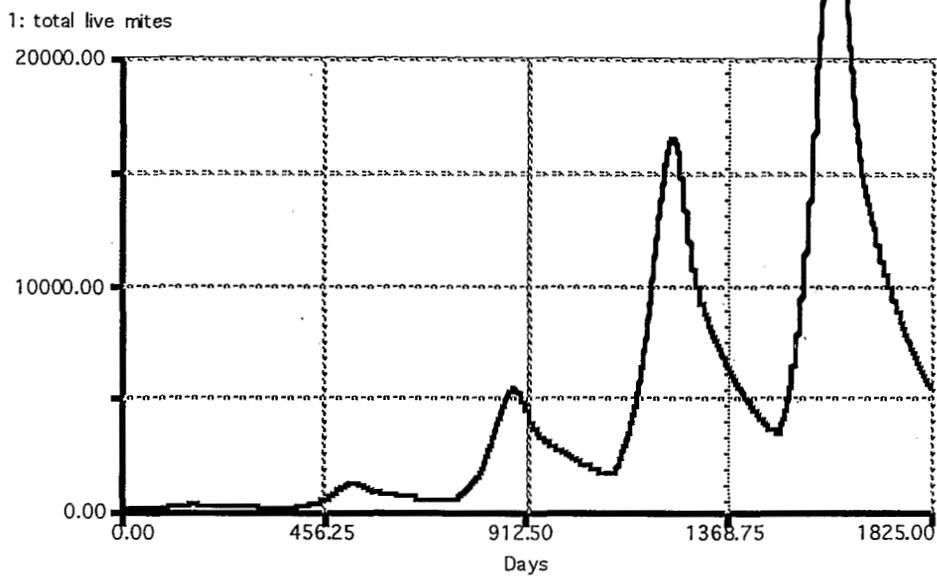


Fig. 4. Simulation of *Varroa* population development (Background data from Fries *et al.*, 1994; mite fertility on worker brood 0.85).

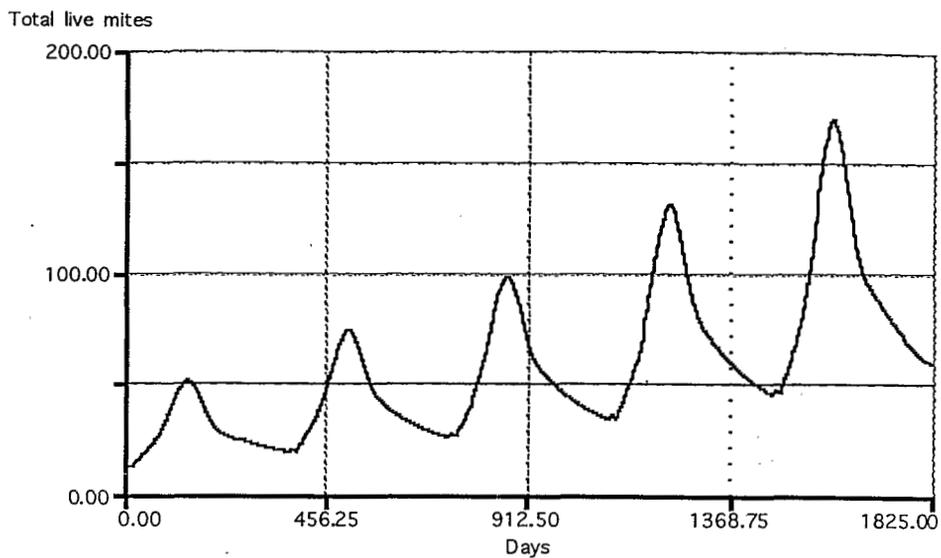


Fig. 5. Simulation of *Varroa* population development (Background data from Fries *et al.*, 1994; mite fertility on worker brood 0.5).

For successful modelling of the mite population dynamics in a certain location, several aspects of both mite and bee biology need to be understood. For the reproductive success of the mite it is necessary to know in detail the brood rearing dynamics over time for a specific region, including distribution of drone and worker brood. Where brood rearing occurs most of the year, the mite may build detrimental population levels within one year (Calatayud and Verdú, 1992), whereas this process may take up to four years in a colder climate with more limited brood rearing (Korpela *et al.*, 1993). Thus, reliable brood rearing data are necessary.

If brood availability and mite fertility may be the key parts in the producing part of the model, the winter mortality of bees is the central factor reducing mite levels in a temperate climate model for *Varroa* population dynamics. Data from Fries *et al.* (1991) show that there are similar numbers of mites found on live bees and on dead bees that fall from the wintering cluster, suggesting that mites do not leave a dying host. There is a uniform distribution of mites on winter bees (Ritter *et al.*, 1989) and mortality of 50% of the wintering bees is normal in a cold climate (Avitabile, 1978), thus reducing mite numbers with as much as 50% over winter due to bee mortality only. Under conditions where you have little or no winter mortality of bees, the only mites lost with the bees are lost with field bees. When brood rearing occurs, the mites are not randomly distributed among the bees, but prefer the younger house bees that stay in the hive (Kraus *et al.*, 1986). This suggests that the mite mortality is significantly lower in a warm climate compared to more temperate conditions. There is extensive data available on mite mortality inside bee hives, based on debris counts, from the Mediterranean region (Calatayud and Verdú, 1993; Calatayud and Verdú, 1995). However, some mites that die inside the colony may be thrown out before they reach the hive bottom, and some mites are also lost outside the colonies when infested bees do not return from the field. These aspects probably need to be quantified sufficiently before a mathematical model for the *Varroa* mite in the Mediterranean region can be obtained.

Model limitations

No mathematical model will produce good results without reliable input data. This general limitation of mathematical modelling is self evident, but sometimes forgotten. A model of a complex system can never be more than an approximation, even with good background data, and should be used accordingly.

One limitation of the model presented earlier (Fries *et al.*, 1994) and later improved as indicated here, is the lack of mite effects on the bees in the models. At low mite levels it is generally accepted that the influence from the mite on the host is very limited. At high infestation levels, however, the presence of the mites will influence the population development of the bees, and thus, create a negative feedback on the population development of the mite. The present model is relevant only as long as the mite has no significant negative influence on the host. In a cold climate, this period may stretch over several years, whereas this influence from the parasite comes much faster in regions with extended brood rearing. Our understanding of the dynamics around colony decline and collapse is probably too limited at present to justify a mathematical model of this phase. We believe that secondary infections are important, but we know nothing about the dynamics of these infections. Nor do we know if certain

mite levels always provoke the same condition or if the impact of secondary infections may vary between colonies, races, seasons or regions.

Uses for a mite population dynamics model

Even if we accept the limitations mentioned above, a well constructed model can still be used for a variety of purposes. The most obvious is of course to mimic treatments for *Varroa* control. Control of the mite population needs to be employed before the mite has any significant effect on the host. Using the computer we can test when it is most advantageous to interfere with the mite population build up and what level of control that is necessary to achieve to avoid a long-term population growth. Such scenarios can easily be tested for example under a variety of outside infestation pressures.

A sensitivity analysis of a model unravels where the system is most sensitive to changes in parameter values. This can be used to understand where breeding efforts may prove most useful to achieve increased mite tolerance. From model simulations it is clear that if we can influence the mite fertility on worker brood (e.g. increase the proportion of infertile mites) the bees have a much better chance to tolerate the infestation. No other characteristic seems to have the same potential.

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