Predicting reproduction rate of varroa

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ABSTRACT

A single equation is derived to predict population–density effects on the reproduction rate of the honey bee parasite *Varroa destructor* Anderson and Trueman. This equation provides a simpler alternative to the approach currently used in the literature, and additionally corrects an anomaly in that approach. The method is then extended to the case of co-existing haplotypes of *Varroa*. It thus derives an equation used without proof for modelling biocontrol of *Varroa*, and examines the error caused by an approximation necessary for a closed form solution. Additionally a varroa population model incorporating the derived equation is described.

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1. Introduction

Varroa destructor Anderson and Trueman is an ectoparasite of the Eastern honey bee (*Apis cerana* Fabricius) in mainland Asia. It was reclassified as a different species from *V. jacobsoni* Oudemans at the turn of the century (Anderson and Trueman, 2000). Six haplotypes of *V. destructor* were identified from mitochondrial DNA, and two of these, the 'Korea' ('Russian') and 'Japan' haplotypes, have transferred to the Western honey bee, *Apis mellifera* Linnaeus (Anderson, 2000; Anderson and Trueman, 2000).

The life cycle of *V. destructor* (varroa) has been extensively reviewed (for example by Sammataro et al., 2000). Varroa feeds on the haemolymph of both adult bees and brood, and reproduces on the latter. A reproducing mite enters a prepupal brood cell shortly before capping and commences egg-laying post capping. The progeny grow and mate inside the cell. Mature females exit with the bee when it emerges, while males and immature females perish. Mites outside brood cells are usually found on adult bees, and are referred to as phoretic.

Varroa causes a number pathologies of both adult bees and brood (see Rosenkranz et al., 2010), often by vectoring viruses (Bowen-Walker et al., 1999; Shen et al., 2005; Chen and Seide, 2007; Gisder et al., 2009). European strains of *A. mellifera* show little tolerance to varroa (de Guzman et al., 1999) which has destroyed huge numbers of colonies in most countries where European *A. mellifera* is kept (see Martin, 1998). Colony survival requires regular control of the mite, most commonly with synthetic or organic chemicals (see Goodwin and van Eaton, 2001).

In addition to causing significant damage to beekeeping in a number of countries (Sammataro et al., 2000), varroa has economic implications for horticultural and arable industries dependent on honeybee pollination (Morse and Calderone, 2000; Cook et al., 2007). In New Zealand, the main, long-term economic impact of varroa will be on the pastoral industries as a loss of feral honey bees leads to a decline in clover (Simpson, 2003).

Population modelling has become established as a useful research tool in the management of varroa. Fries et al. (1994) published the first varroa population model which was later refined by Callis et al. (1999). Subsequent models have been used for improving varroa-management to maintain colony health (Martin, 1999; DeGrandi-Hoffman and Curry, 2004), investigating viral spread and colony collapse (Martin, 2001; Sumpter and Martin, 2004), tailoring programmes to breed varroa-resistance in honey bees (Wilkinson and Smith, 2002), and investigating whether a hypothetically benign haplotype of varroa could be used as a competitive antagonist for the biological control of pathogenic strains (Vetharaniam and Barlow, 2006).

The need to account for population density effects on varroa reproduction rates was recognised by Fuchs and Langenbach (1989) and first addressed in a varroa growth model by Martin (1998). As the mite population increases, so does the incidence of multiple females reproducing in the same cell, which increases offspring mortality. To predict the total mite production Martin (1998) first approximated the fraction of available cells invaded by 0, 1, 2, 3 or 4 mother mites (z) using the Poisson distribution ($e^{-m}m^z/z!$), where the Poisson parameter (m) is the ratio of invading mites to available cells. From here further steps were taken, which included the use

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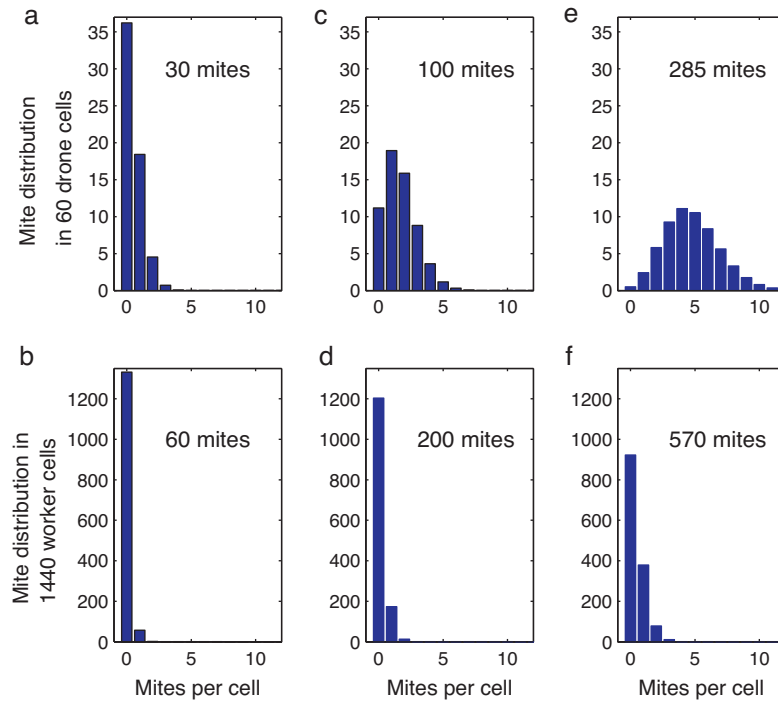
Fig. 1. Distribution of mites in cells when the invasion is a random, binomial process, as predicted by Eq. (3). The number of mites invading are given in each panel for 60 drone cells (top panels) and 1390 worker cells (bottom panel), and were calculated for a colony of 60,000 bees with phoretic mite infestation levels of 1% (panels a and b), 3.5% (panels c and d) and 10% (panels e and f).

of individual multipliers that gave relative reproduction rates for each value of z. The approach was adopted by Wilkinson and Smith (2002).

This paper provides a easier alternative by deriving a single equation that estimates the number of mites emerging from cells each day:

$$E = \sigma\nu \left[1 + \gamma \left(1 - \frac{r}{\mu} \right)^{\nu-1} \right] \qquad (1)$$

This equation must be applied to worker cells and drone cells separately. μ is the number of either worker or drone cells available for invasion and ν is the number of varroa invading these cells per day. γ is respectively 1.06 and 2.44 for worker and drone cells, and is the reproduction rate of a singleton mother. r reflects the effect of multiple cell invasion, and is respectively 0.156 and 0.131 for worker and drone cells. σ is the survival rate of the invading mites and their offspring that emerge from the cells, and is 0.62 and 0.78 respectively for worker and drone cells (Wilkinson and Smith, 2002). Simulations of population growth must allow a delay between cell invasion and mite emergence. This is nominally 13 days for worker cells and 16 days for drone cells (Vetharaniam and Barlow, 2006).

Eq. (1) is then extended to the case when the Japan and Korea haplotypes co-exist in the same colony. These haplotypes will interbreed but show a post-zygotic reproductive isolation that varies between populations (Solignac et al., 2005). The formula derived below for the reproduction of interacting haplotypes has been used by Vetharaniam and Barlow (2006) without proof. Thus this paper also addresses that omission.

2. Method and calculations

2.1. Reproduction involving a single varroa haplotype

The number of varroa that enter brood cells is governed by the ratio of suitable brood cells to the number of adult bees, and by the

number of phoretic mites (Boot et al., 1995). Wilkinson and Smith (2002) give formulae to estimate these invasion rates, with drone cells being 11.6 times more likely to be invaded than worker cells.

Suppose that for any given day we have μ_D drone cells and μ_W worker cells suitable for invasion, and that there are invaded by ν_D and ν_W mites respectively. For simplicity of notation we can drop the subscript and refer to these as μ cells suitable for invasion and ν invading mother mites.

These mites will invade the cells randomly (Martin, 1998) and by assumption show no preference between cells of a particular type. Then, considering varroa distribution in either drone or worker cells, the number of mites in each cell ($x_1, \ldots, x_\mu$, say) will have a multinomial distribution with associated probabilities $\theta_i = 1/\mu$, and number of invading mother mites ν.

Fuchs and Langenbach (1989) found that the reproduction rate per mite declined exponentially as the number of mother mites per cell increased. This pattern is consistent with data from other studies, tabulated by Martin (1995). We can then write the number of new mites produced in a cell with x invading mites as

$$V_c(x) = \gamma x e^{a(1-x)}, \quad x = 1, 2, \ldots \qquad (2)$$

where γ is the reproduction rate of a mite when it is alone it its cell, and a reflects the decline in reproduction rate as the number of mothers in a cell increases. For drone brood, $\gamma = \gamma_D$ and $a = a_D$; for worker brood, $\gamma = \gamma_W$ and $a = a_W$.

The average number of mites produced in all the cells could be predicted by summing Eq. (2) over $x_1, \ldots, x_\mu$, weighting it by the corresponding multinomial probability, and then summing the result over all possible permutations of $x_1, \ldots, x_\mu$. This calculation would involve summation over $\mu - 1$ nested levels, and is far from appealing.

However the problem can be converted into a simpler calculation involving the binomial distribution as follows. For any given cell, the probability that a given mite will enter it is $\theta = 1/\mu$ and $1 - \theta$ that it will not. Thus the number of invading mites, x, in a given cell