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ORIGINAL ARTICLE

Behaviours of honeybees can reduce the probability of deformed wing virus outbreaks in *Varroa destructor*-infested colonies

Francis Mugabi[1] · Kevin J. Duffy[1] · Frank van Langevelde[2]

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Abstract

Honeybees are important plant pollinators. Unfortunately, there is a growing increase in the loss of honeybee colonies, and this is having a serious economic impact on crop farmers. A major cause of these losses is the parasitic mite *Varroa destructor*, which is a vector of deformed wing virus (DWV). Some bee species have resistant mechanisms, such as grooming and hygienic behaviours, against *Varroa* mites. A clear understanding of the effects of these control behaviours on the mites and the viruses they transmit can be important in reducing colony losses. Here, a stochastic model is formulated and analysed to consider the extent to which these control behaviours reduce the probability of an outbreak of DWV in honeybee colonies. Vector and bee-to-bee transmission routes are considered. Using branching process theory, it is shown that without any hygienic or grooming behaviour, a large probability of a DWV outbreak is possible. Also, if bees apply grooming or hygienic behaviour, this can reduce the probability of a virus outbreak, especially in the case of vector transmission, where it can be reduced to zero. Hygienic behaviour is the most significant factor in reducing a DWV outbreak. Thus, bee selection for hygienic behaviour may be important to reduce honeybee colony losses caused by DWV.

Keywords Grooming behaviour · Hygienic behaviour · *Varroa destructor* · DWV · Branching process

Introduction

Bees are an important crop pollinator worldwide (Hung et al. 2018; Russo et al. 2020) and a source of profitable hive products for the apiculture industry (Russo et al. 2020; Klein et al. 2007). However, honeybee colony losses are on the rise, as reported in South Africa (Pirk et al. 2014), Oceania (Brown et al. 2018), the Northern Hemisphere (vanEngelsdorp et al. 2011), and South America (Requier et al. 2018). Among the reasons for colony losses are parasites, pesticides, climate change, and diseases (Russo et al. 2020; Goulson et al. 2015). The main parasite affecting honeybees, especially those of European origin, is the mite *Varroa-destructor* (Rosenkranz et al. 2010). These mites feed on the body fat of both adult and immature bees in the brood stage (larvae and pupae), which reduces their fitness and lifespan (Ramsey et al. 2019). Heavily mite-infested colonies, if left untreated, can collapse (Martin 1994). However, it is believed that in most cases, the ultimate cause of colony collapse is not the mites but the pathogens that they transmit to the bees (Rosenkranz et al. 2010; Moore et al. 2015). One of the most serious pathogens vectored by *Varroa destructor* is deformed wing virus (DWV) (Bowen-Walker et al. 1999). DMV can cause shortened abdomens, deformed wings, and even death (Yue and Genersch 2005). The virus is widely distributed in bee colonies across Asia, Africa, and Europe (Allen and Ball 1996), and it has been associated with the collapse of colonies in the United Kingdom (Martin et al. 1998).

The survival of some bee species, like the European honeybee (*Apis mellifera*), depends on mite control (Fries et al. 1996), and without periodic treatment using miticides or other substances, colonies can collapse within one growing

✉ Kevin J. Duffy
kevind@dut.ac.za

Francis Mugabi
francism@dut.ac.za

Frank van Langevelde
frank.vanlangevelde@wur.nl

[1] Institute of Systems Science, Durban University of Technology, 4-43 M L Sultan Road, P. O. Box 1334, Durban 400, KwaZulu-Natal, South Africa

[2] Wildlife Ecology and Conservation Group, Wageningen University and Research, P. O. Box 47, Wageningen 6700 AA, The Netherlands

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season (Rosenkranz et al. 2010). However, the application of miticides can have negative impacts on bee populations (Gregorc and Bowen 2000) and may lead to the development of resistant mites (Milani 1999). Natural substances such as botanical oils and organic acids can be used, but they are not very effective in controlling mites (Rosenkranz et al. 2010).

Several honeybee species have adapted and coexisted with mites without the need for any control measures (Nganso et al. 2017). These species include the Asian honeybee (*Apis cerana*) (Fries et al. 1996), and African subspecies of *Apis mellifera*, such as the South African Cape honeybee (*Apis mellifera capensis*) and the Savannah honeybee (*Apis mellifera scutellata*). The most likely natural resistance mechanisms behind such coexistence are grooming and *Varroa*-sensitive hygienic behaviours (Nganso et al. 2017; Kruitwagen et al. 2017; Panziera et al. 2017). *Varroa*-sensitive hygienic behaviour takes place when adult worker bees are aware of the existence of mite offspring in brood cells and kill these infected cells as a means of stopping them or their pathogens from spreading in the colony (de Figueiró et al. 2016). In grooming behaviour, adult worker bees use their mandibles and legs to remove, injure, or kill mites from their bodies (de Figueiró et al. 2016).

Various studies have demonstrated the effectiveness of grooming and hygienic behaviours in keeping the population of mites in bee colonies at low levels (Russo et al. 2020; Fries et al. 1996; Nganso et al. 2017; de Figueiró et al. 2016; Pritchard 2016; Torres and Torres 2020). However, it is not clear if these bees natural defence mechanisms against mites can be enough to control an outbreak of viruses, specifically DWV, in *Varroa*-infested colonies. Thus, in this study, a stochastic model is used to study the effects of the hygienic and grooming behaviours of honeybees on the outbreak or extinction of DWV in *Varroa*-infested colonies.

Mathematical models have been used to study the effects of mites and the viruses they transmit on honeybee colonies. One of the first models of bee interactions with mites and viruses, using differential equations, was developed by Sumpter and Martin (2004) to explore the relationship between mite load and the occurrence of a virus epidemic. Eberl et al. (2010) by extending the model in Sumpter and Martin (2004), analysed the importance of brood maintenance terms for bees and the effects of seasonality on the dynamics of acute paralysis virus (APV). Ratti et al. (2012) modified the model in Eberl et al. (2010) by introducing a logistic growth of mites and mite-induced death rate to derive the conditions under which the bee colony can fight off an APV epidemic. Ratti et al. (2015) adopted the framework in Ratti et al. (2012) to study the effects of seasonality on a colony. Kang et al. (2016) used a deterministic model to examine the effects of parasitism, allee effects, and different virus transmission modes. Ratti et al. (2017) modified the model in Ratti et al. (2015) to investigate the interplay between forager loss and disease infestation. Dénes and Ibrahim (2019) formulated an ordinary differential equations model to identify the key variables that determine the conditions for honeybee colony survival or collapse in the presence of mites and an associated virus. Britton and Jane White (2021) explored the effects of covert and overt infections on the dynamics of DWV. The authors in

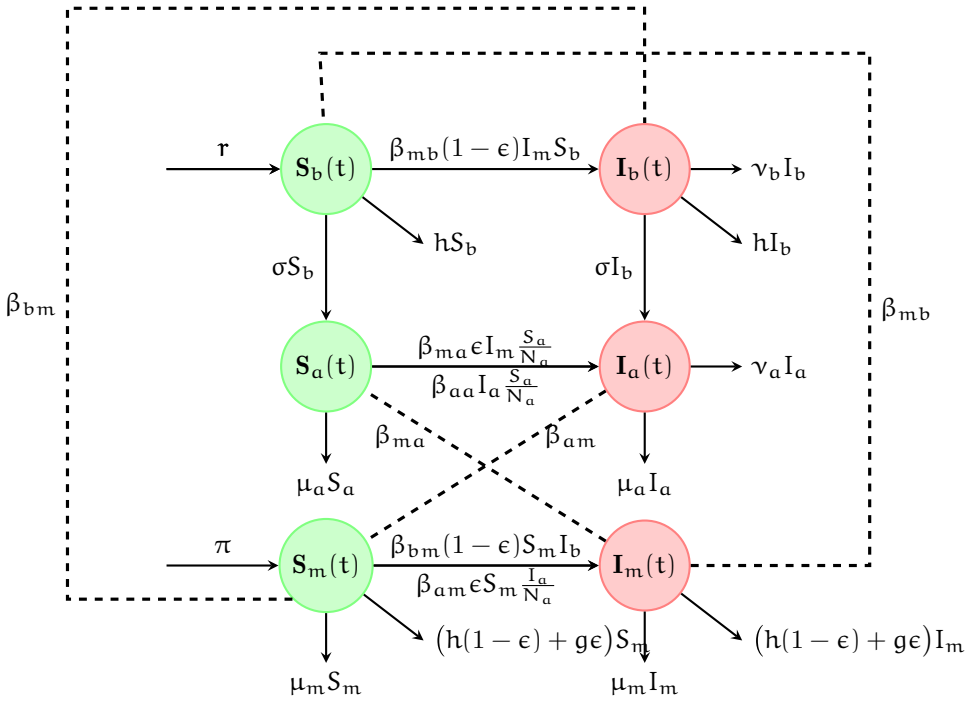

Fig. 1 Transmission dynamics of DWV in a honeybee colony infested with *Varroa* mites

Table 1 Parameter description, values, units, and sources

Parameter	Description	Value	Unit	References
r	Average number of eggs laid by the queen	1500	Eggs day^{-1}	(Sumpter and Martin 2004)
β_{mb}	Infection rate of a pupa by the mites	0.0003	Pupa day^{-1}	(Kang et al. 2016)
ϵ	Proportion of mites in the phoretic stage	0.25	Dimensionless	(Torres and Torres 2020)
σ	Maturation rate of pupa	1/12	Day^{-1}	(Sumpter and Martin 2004)
h	Hygienic rate	[0,1]	Day^{-1}	Varied
β_{ma}	Infection rate of adult bees by the mites	0.12	Day^{-1}	(Kang et al. 2016)
β_{aa}	Transmission rate between adult bees	0.3	Day^{-1}	(Kang et al. 2016)
μ_a	Natural mortality rate of adult bees	1/25	Day^{-1}	(Sumpter and Martin 2004)
ν_a	Virus-induced mortality rate of adult bees	0.04	Day^{-1}	(Sumpter and Martin 2004)
ν_b	Virus-induced mortality rate of pupa	0.2	Day^{-1}	(Martin 2001)
β_{bm}	Infection rate of mites by pupa	0.0003	Mite day^{-1}	(Kang et al. 2016)
β_{am}	Infection rate of mites by adult bees	0.12	Day^{-1}	(Kang et al. 2016)
μ_m	Natural mortality rate of mites	1/27	Day^{-1}	(Torres and Torres 2020)
μ_m				
π	Recruitment rate of mites	12	Mite day^{-1}	Assumed
g	Grooming rate	[0, 1]	Day^{-1}	Varied

The parameters β_{am}, β_{ma}, β_{bm}, and β_{mb} are estimated from the study by Kang et al. (2016) such that $\beta_{am}\epsilon = 0.03$, $\beta_{ma}\epsilon = 0.03$, and $\beta_{mb} = \beta_{bm} = c\alpha$, where $\alpha = 0.05$ and $c = 0.005$ are parasitism rate and conversion rate of nutrients obtained from pupa to mite reproduction sustenance, respectively

Sarathi Mandal and Maity (2022) considered a stochastic version of the model in Kang et al. (2016) to study the effects of demographic variability on disease dynamics in a bee colony. These models provide an understanding of the dynamics of mites, bees, and viruses. However, to our knowledge, no models have been developed to consider the effects of grooming and/or hygienic behaviour on the outbreak or extinction of DWV.

In this study, an ordinary differential equation (ODE) model is formulated in Sect. 2.1 by modifying the model in Kang et al. (2016) by including grooming and hygienic parameters. In addition, variables for the brood population (S_b and I_b) are included in order to track the effects of *Varroa*-sensitive hygienic behaviour. The effects of parasitism and allee effects are not considered since they are extensively studied in Kang et al. (2016). Since deterministic models do not account for stochasticity in transmission dynamics, which is important in determining the probability of disease outbreak or extinction (Lahodny Jr et al. 2015), a stochastic version of the ODE model in Sect. 2.1 is derived and analysed in Sect. 2.2.

Methods

ODE model description

An ODE model for the dynamics of DWV in a honeybee colony consisting of brood (larva and pupa), adult bees, and *Varroa* mites is developed. The virus dynamics of brood, adult bees, and mite populations are modelled by the classical susceptible-infectious (SI) epidemic process. The brood, adult bee, and mite total populations are respectively given by $N_b(t) = S_b(t) + I_b(t)$, $N_a(t) = S_a(t) + I_a(t)$, and $N_m(t) = S_m(t) + I_m(t)$, where a, b, and m refer to brood, adult bees, and mites. For the mite population, a proportion $\epsilon \in [0, 1]$ of mites are taken to be in the phoretic stage, and as such, $1 - \epsilon$ are in the reproductive stage.

Table 2 State transitions and their rates for the different events of the CTMC model for DWV dynamics in a honeybee-mite-infested colony

Event	State transition, $\Delta(\vec{V}(t))$	Rate of occurance, λ
Birth of S_b	$S_b \to S_b + 1$	r
Infection of S_b	$(S_b, I_b) \to (S_b - 1, I_b + 1)$	$\beta_{mb}(1-\epsilon)I_m S_b$
Maturation of S_b	$(S_b, S_a) \to (S_b - 1, S_a + 1)$	σS_b
Death of S_b	$S_b \to S_b - 1$	hS_b
Maturation of I_b	$(I_b, I_a) \to (I_b - 1, I_a + 1)$	σI_b
Death of I_b	$I_b \to I_b - 1$	$(h + \nu_b)I_b$
Infection of S_a by I_m	$(S_a, I_a) \to (S_a - 1, I_a + 1)$	$\beta_{ma}\epsilon I_m \frac{S_a}{N_a}$
Infection of S_a by I_a	$(S_b, I_a) \to (S_a - 1, I_a + 1)$	$\beta_{aa} I_a \frac{S_a}{N_a}$
Death of S_a	$S_a \to S_a - 1$	$\mu_a S_a$
Death of I_a	$I_a \to I_a - 1$	$(\nu_a + \mu_a)I_a$
Birth of S_m	$S_m \to S_m + 1$	π
Infection of S_m by I_a	$(S_m, I_m) \to (S_m - 1, I_m + 1)$	$\beta_{am}\epsilon S_m \frac{I_a}{N_a}$
Infection of S_m by I_b	$(S_m, I_m) \to (S_m - 1, I_m + 1)$	$\beta_{bm}(1-\epsilon)S_m I_b$
Death of S_m	$S_m \to S_m - 1$	$\big(h(1-\epsilon) + g\epsilon + \mu_m\big)S_m$
Death of I_m	$I_m \to I_m - 1$	$\big(h(1-\epsilon) + g\epsilon + \mu_m\big)I_m$

The expression $\lambda\Delta t + o(\Delta t)$ is the infinitesimal transition probability for the change $\Delta\vec{V}(t) = \vec{V}(t + \Delta t) - \vec{V}(t)$

The brood population is assumed to be recruited at a constant rate r, equivalent to the egg-laying rate of the queen per day. Since we are not considering the effects of seasonality, the brood is considered to be reared to maximum capacity, independent of colony size (Sumpter and Martin 2004). Mites in the reproductive stage enter brood cells before capping for reproduction, where they feed on the brood hemolymph. Parasitized brood can be infected by infectious mites at a rate $\beta_{mp}(1-\epsilon)I_m S_p$. According to Chen et al. (2006), there is a linear relationship between the number of mites to which brood is exposed and the virus frequency. That is, the more mites introduced per cell, the greater the incidence of virus in brood. This indicates that the virus transmission rate from mites to brood is density-dependent. Adult bees can kill infested brood to prevent mites from spreading in a colony at a rate h, a behaviour known as *Varroa*-sensitive hygiene. Infected brood can die due to the virus at a rate ν_b, and the brood that survives death can emerge as adults at a rate σ independent of the virus status.

Susceptible adult bees can be infected by phoretic mites at a rate $\beta_{ma}\epsilon I_m \frac{S_a}{N_a}$ or by infectious bees at a rate $\beta_{aa} I_a \frac{S_a}{N_a}$ through trophallaxis. Following the studies in Ratti et al. (2012), Kang et al. (2016), Sarathi Mandal and Maity (2022), a frequency-dependent transmission approach is used. Adult bees can die naturally at a rate μ_a, or for those in the infectious class, due to the virus, at a rate ν_a. For the mite population, it is assumed that susceptible mites are recruited by birth at a constant rate π. Susceptible mites in the phoretic stage can be infected by adult bees at a rate $\beta_{am}\epsilon S_m \frac{I_a}{N_a}$, and those in the reproductive stage can be infected by the brood at a rate $\beta_{pm}(1-\epsilon)S_m I_p$. Frequency- and density-dependent transmission approaches are used accordingly, as used in Kang et al. (2016). Mortality of mites can be due to natural causes at a rate μ_m or to grooming (a behaviour where adult bees injure or kill phoretic mites attached to their bodies) at a rate g. It can be assumed that the mites on a bee die if the bee is groomed (Torres and Torres 2020). Based on these assumptions and definitions, the flow diagram for the transmission dynamics of DWV in a honeybee colony infested by mites is shown in Fig. 1.

From Fig. 1, the system of equations for the transmission dynamics of the virus is given by

$$\begin{aligned}
\frac{dS_b}{dt} &= r - \beta_{mb}(1-\epsilon)I_m S_b - (\sigma + h)S_b,\\
\frac{dI_b}{dt} &= \beta_{mb}(1-\epsilon)I_m S_b - (\sigma + h + \nu_b)I_b,\\
\frac{dS_a}{dt} &= \sigma S_b - \beta_{ma}\epsilon I_m \frac{S_a}{N_a} - \beta_{aa} I_a \frac{S_a}{N_a} - \mu_a S_a,\\
\frac{dI_a}{dt} &= \sigma I_b + \beta_{ma}\epsilon I_m \frac{S_a}{N_a} + \beta_{aa} I_a \frac{S_a}{N_a} - (\nu_a + \mu_a)I_a,\\
\frac{dS_m}{dt} &= \pi - \beta_{bm}(1-\epsilon)S_m I_b - \beta_{am}\epsilon S_m \frac{I_a}{N_a}\\
&\quad - \big(h(1-\epsilon) + g\epsilon + \mu_m\big)S_m,\\
\frac{dI_m}{dt} &= \beta_{bm}(1-\epsilon)S_m I_b + \beta_{am}\epsilon S_m \frac{I_a}{N_a}\\
&\quad - \big(h(1-\epsilon) + g\epsilon + \mu_m\big)I_m,
\end{aligned} \tag{2.1}$$

with initial conditions $S_b > 0$, $I_b \geqslant 0$, $S_a > 0$, $I_a \geqslant 0$, $S_m > 0$, and $I_m \geqslant 0$. The model parameters are summarised in Table 1.

The disease-free equilibrium, which is obtained by setting the right-hand side of the model (2.1) to zero, is given by $(S_b^*, I_b^*, S_a^*, I_a^*, S_m^*, I_m^*) = \left(r/(\sigma+h), 0, r\sigma/(\sigma+h)\mu_a, 0, \pi/\left(h(1-\epsilon)+g\epsilon+\mu_m\right), 0\right)$. Stability analyses of model (2.1) are possible, but as mentioned in Section 1, the ODE does not account for stochasticity in the transmission dynamics, which is important in determining the probability of disease extinction or a major outbreak (Lahodny Jr et al. 2015). Thus, in the next section, a continuous-time Markov Chain (CTMC) stochastic version of the ODE model (2.1) is derived. In Section 3, numerical results of Model (2.1) are provided for comparison.

CTMC model

A CTMC model for (2.1) is formulated. Let $S_b(t)$, $I_b(t)$, $S_a(t)$, $I_a(t)$, $S_m(t)$, and $I_m(t)$ denote the discrete-valued random variables for brood, adult bees, and mite subpopulations at time $t \in [0, \infty)$. For convenience, the notation used in (2.1) is maintained. Let

$$\vec{V}(t) = \left(S_b(t), I_b(t), S_a(t), I_a(t), S_m(t), I_m(t)\right) \tag{2.2}$$

be the associated random vector. In a CTMC model, transition from one state to another can occur at any time (Maliyoni et al. 2019). The state transitions and the rate at which they occur for the CTMC model are given in Table 2.

The time between events is exponentially distributed as a result of the assumption that the process has the Markov property (Lahodny Jr et al. 2015; Maliyoni et al. 2019) with the parameter

$$\begin{aligned}\tau(\vec{V}) = {} & r + \left\{\beta_{mb}(1-\epsilon)I_m + \sigma + h\right\}S_b + (\sigma + h + \nu_b)I_b \\ & + \left\{\beta_{ma}\epsilon I_m + \beta_{aa}I_a\right\}\frac{S_a}{N_a} + \mu_a N_a + \nu_a I_a \\ & + \pi + \left\{h(1-\epsilon) + g\epsilon + \mu_m\right\}N_m \\ & + \left\{\beta_{am}\epsilon\frac{I_a}{N_a} + \beta_{bm}(1-\epsilon)I_b\right\}S_m.\end{aligned} \tag{2.3}$$

To derive the expression for the probability of DWV extinction or outbreak, multitype branching process theory is used.

Branching process

The behaviour of the CTMC model near the disease-free equilibrium is studied to find out if a major outbreak of DWV can take place when a few infectious bees (brood or adult) or mites are introduced into a honeybee colony. The probability of a major outbreak or extinction for the CTMC model near disease-free equilibrium can be estimated by applying multitype branching process theory (Allen 2017). The theory assumes that the rates in Table 2 are linear, the susceptible subpopulations (S_b, S_a, and S_m) are at disease-free, births and deaths are independent, and the process is time-homogeneous (Lahodny Jr et al. 2015). By these assumptions, the offspring probability generating functions (pgfs) for infectious subpopulations (I_b, I_a, and I_m) can be derived (Lahodny Jr et al. 2015; Maliyoni et al. 2019). The term birth means a new infection, and offspring means the number of new infections. Offspring pgfs are used to determine the probability of a major outbreak or extinction.

Define $I = (I_b, I_a, I_m)^T$ as a vector of infectious brood, adult bees, and mite subpopulations. Assume that infected bees (brood or adult) or mites of type i, I_i, give birth to bees or mites of type j, I_j and that the number of offspring produced by a bee or a mite of type i does not depend on the number of offspring produced by other bees or mites of type i or j (Maliyoni et al. 2019). Let $\{X_{ji}\}_{j=1}^3$ be the offspring random variables for type i, $i = 1, 2, 3$, where X_{ji} denotes the number of offspring of type j produced by bees or mites of type i (Lahodny Jr et al. 2015; Maliyoni et al. 2019). Also, let the probability that an infected bee or mite of type i gives birth to k_j bees or mites of type j be

$$P_i(k_1, k_2, k_3) = \text{prob}(X_{1i} = k_1, X_{2i} = k_2, X_{3i} = k_3). \tag{2.4}$$

Then, the offspring pgf for bees or mites of type i given that $I_i(0) = 1$ and $I_j(0) = 0$, $i \neq j$, $f_i\colon [0,1]^3 \to [0,1]$ is

$$\begin{aligned}f_i(x_1, x_2, x_3) = {} & \sum_{k_3=0}^{\infty}\sum_{k_2=0}^{\infty}\sum_{k_1=0}^{\infty} \\ & P_i(k_1, k_2, k_3)(x_1)^{k_1}(x_2)^{k_2}(x_3)^{k_3},\end{aligned} \tag{2.5}$$

for $x_i \in \mathbb{R}$.

Initially, when the susceptible subpopulations are near the disease-free equilibrium, $S_b(0) \approx N_b(0) = S_b^*$, $S_a(0) \approx N_a(0) = S_a^*$ and $S_m(0) \approx N_m(0) = S_m^*$, then the specific offspring pgfs for I_b, I_a, and I_m can be derived using (2.5) and the rates in Table 2 (Lahodny Jr et al. 2015).

The offspring pgf for an infectious brood such that $I_b(0) = 1$, $I_a(0) = 0$ and $I_m(0) = 0$ is given by

$$\begin{aligned}& f_1(x_1, x_2, x_3) \\ & \quad = \frac{\sigma x_2 + \beta_{bm}(1-\epsilon)S_m^* x_1 x_3 + h + \nu_b}{\sigma + \beta_{bm}(1-\epsilon)S_m^* + h + \nu_b}.\end{aligned} \tag{2.6}$$

In (2.6), an infectious brood either matures to become an infectious adult bee at a probability of $\sigma/\left(\sigma + \beta_{bm}(1-\epsilon)S_m^* + h + \nu_b\right)$ or infects a susceptible mite with a probability of $\beta_{bm}(1-\epsilon)S_m^*/\left(\sigma + \beta_{bm}(1-\epsilon)S_m^* + h + \nu_b\right)$, or dies with a probability of $(h + \nu_b)/\left(\sigma + \beta_{bm}(1-\epsilon)S_m^* + h + \nu_b\right)$.

The offspring pgf for an infectious adult bee such that $I_b(0) = 0$, $I_a(0) = 1$ and $I_m(0) = 0$ is given by

$$f_2(x_1,x_2,x_3)=\frac{\beta_{aa}x_2^2+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}x_2x_3+\mu_a+\nu_a}{\beta_{aa}+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}+\mu_a+\nu_a}. \tag{2.7}$$

In (2.7), an infectious adult bee infects a susceptible adult bee with a probability of $\beta_{aa}/\left(\beta_{aa}+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}+\mu_a+\nu_a\right)$ or infects a mite with a probability of $\beta_{am}\epsilon\frac{S_m^*}{S_a^*}/\left(\beta_{aa}+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}+\mu_a+\nu_a\right)$ or dies with probability of $(\mu_a+\nu_a)/\left(\beta_{aa}+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}+\mu_a+\nu_a\right)$.

The offspring pgf for an infectious mite such that $I_b(0)=0$, $I_a(0)=0$ and $I_m(0)=1$ is given by

$$f_3(x_1,x_2,x_3)=\frac{\beta_{mb}(1-\epsilon)S_b^*x_1x_3+\beta_{ma}\epsilon x_2x_3+h(1-\epsilon)+g\epsilon+\mu_m}{\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon+h(1-\epsilon)+g\epsilon+\mu_m}. \tag{2.8}$$

In (2.8), a mite infects a pupa with a probability of $\beta_{mb}(1-\epsilon)S_b^*/\left(\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon+h(1-\epsilon)+g\epsilon+\mu_m\right)$ or infects an adult bee with a probability of $\beta_{ma}\epsilon/(\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon+h(1-\epsilon)+g\epsilon+\mu_m)$ or dies with a probability of $\left(h(1-\epsilon)+g\epsilon+\mu_m\right)/\left(\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon+h(1-\epsilon)+g\epsilon+\mu_m\right)$.

Table 3 Probability of virus extinction calculated from the branching process. The parameter values used are as given in Table 1 with $h=0$ and $g=0$

			(i)	(ii)
Initial conditions			$\beta_{aa}=0.3$	$\beta_{aa}=0$
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5871	0.7507
0	1	0	0.2664	0.9969
0	0	1	0.0214	0.0354
2	0	0	0.3447	0.5636
0	2	0	0.0710	0.9938
0	0	2	0.0005	0.0013
1	1	1	0.0033	0.0265

From (2.5), the expectation matrix of the offspring pgfs (see (Mugabi et al. 2021) for derivation) is given by

$$\mathbb{E}=\begin{bmatrix}\frac{\beta_{bm}(1-\epsilon)S_m^*}{A_1} & 0 & \frac{\beta_{mb}(1-\epsilon)S_b^*}{A_3}\\ \frac{\sigma}{A_1} & \frac{2\beta_{aa}+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}}{A_2} & \frac{\beta_{ma}\epsilon}{A_3}\\ \frac{\beta_{bm}(1-\epsilon)S_m^*}{A_1} & \frac{\beta_{am}\epsilon\frac{S_m^*}{S_a^*}}{A_2} & \frac{\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon}{A_3}\end{bmatrix}, \tag{2.9}$$

where $A_1=\sigma+\beta_{bm}(1-\epsilon)S_m^*+h+\nu_b$, $A_2=\beta_{aa}+\beta_{am}\epsilon\frac{S_m^*}{S_a^*}+\mu_a+\nu_a$, and $A_3=\beta_{ma}\epsilon+\beta_{mb}(1-\epsilon)S_b^*+h(1-\epsilon)+g\epsilon+\mu_m$.

The spectral radius of $\mathbb{E}$, $\rho(\mathbb{E})$ determines the probability of disease extinction or persistence (Lahodny Jr et al. 2015; Maliyoni et al. 2019; Mugabi et al. 2021). If $\rho(\mathbb{E})\leqslant 1$, the probability of disease extinction is one (Maliyoni et al. 2019; Mugabi et al. 2021). That is,

$$\mathbb{P}_0=\lim_{t\to\infty}Prob\{\vec{I}(t)=\vec{0}\}=1 \tag{2.10}$$

with $\vec{I}(t)=(I_b(t),I_a(t),I_m(t))^{tr}$.

If $\rho(\mathbb{E})>1$,

$$\mathbb{P}_0=\lim_{t\to\infty}Prob\{\vec{I}(t)=\vec{0}\}=x_1^{i_b}x_2^{i_a}x_3^{i_m}<1, \tag{2.11}$$

where $i_b=I_b(0)$, $i_a=I_a(0)$, $i_m=I_m(0)$, and x_1, x_2, and x_3 are obtained from the offspring pgfs (Eqs. (2.6)-(2.8)), such that $f_i(x_1,x_2,x_3)=x_i$, $i=1,2,3$.

The corresponding probability of a major outbreak or persistence is given by

$$\mathbb{P}_m=1-\mathbb{P}_0. \tag{2.12}$$

Solving the system $f_i(x_1,x_2,x_3)=x_i$, $i=1,2,3$ leads to

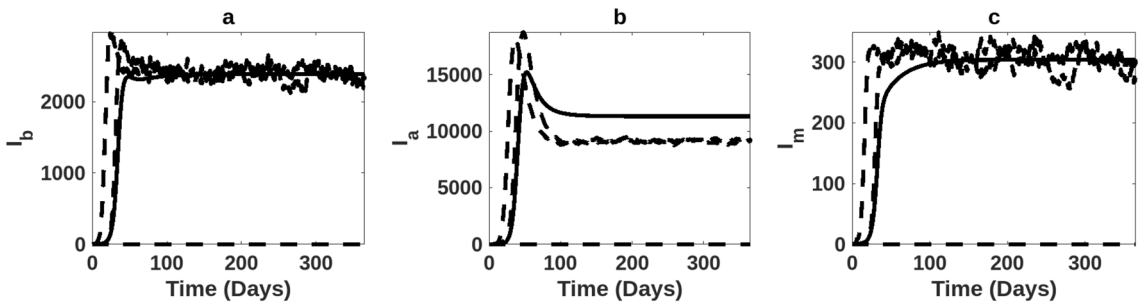

Fig. 2 The ODE solution and sample paths of the CTMC model for some initial conditions in Table 3 illustrating virus extinction or a major outbreak. The parameter values used are as given in Table 1 with $h=g=0$ and $\beta_{aa}=0$. The initial conditions for the ODE model are $S_b=100$, $I_b=1$, $S_a=200$, $I_a=1$, $S_m=50$ and $I_m=1$

$$x_1 = \frac{\beta_{am}\epsilon\frac{S_m^*}{S_a^*}x_2\left(\sigma x_2 + h + \nu_b\right)}{\beta_{am}\epsilon\frac{S_m^*}{S_a^*}A_1x_2 - \beta_{bm}(1-\epsilon)S_m^*\left(A_2x_2 - \beta_{aa}x_2^2 - (\mu_a+\nu_a)\right)},$$
$$x_3 = \frac{A_2x_2 - \beta_{aa}x_2^2 - (\mu_a+\nu_a)}{\beta_{am}\epsilon\frac{S_m^*}{S_a^*}x_2} \quad (2.13)$$

with x_2 satisfying

$$c_5x_2^5 + c_4x_2^4 + c_3x_2^3 + c_2x_2^2 + c_1x_2 + c_0 = 0, \quad (2.14)$$

where

Table 4 Effects of *Varroa*-sensitive hygienic behaviour on the probability of extinction calculated from the branching process. The parameter values used are as given in Table 1 with $h \in [0, 0.16]$ and $g = 0$

			(*i*)			(*ii*)		
Initial conditions			$\mathbb{P}_0$ ($\beta_{aa} = 0.3$)			$\mathbb{P}_0$ ($\beta_{aa} = 0$)		
i_b	i_a	i_m	$h = 0$	$h = 0.08$	$h = 0.16$	$h = 0$	$h = 0.08$	$h = 0.16$
1	0	0	0.5871	0.7661	0.8356	0.7507	0.9494	1.0000
0	1	0	0.2664	0.2665	0.2665	0.9969	0.9987	1.0000
0	0	1	0.0214	0.1611	0.3858	0.0354	0.4815	1.0000

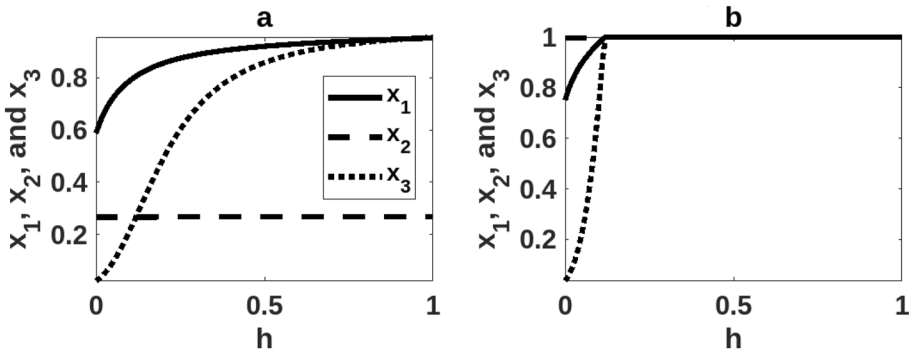

Fig. 3 Effects of *Varroa*-sensitive hygienic behaviour on the probabilities of DWV extinction x_1, x_2, and x_3 in pupae, adult bees, and mites, respectively. The parameter values used are as given in Table 1 with $h \in [0, 1]$, $g = 0$, $\beta_{aa} = 0.3$ for **a**, and $\beta_{aa} = 0$ for **b**

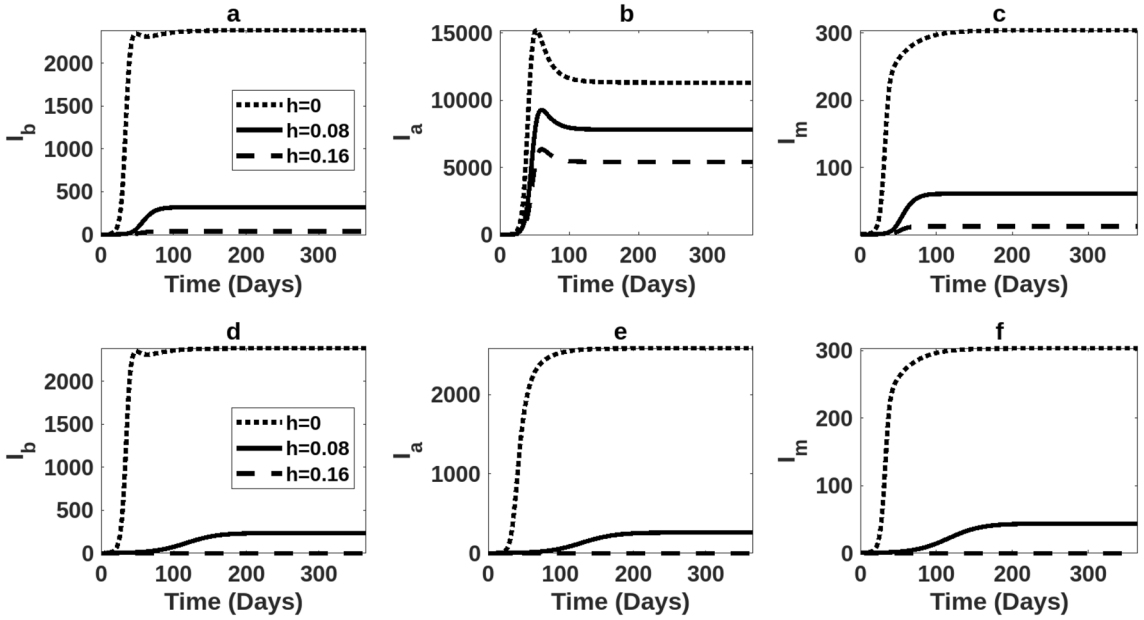

Fig. 4 Effects of varying the hygienic behaviour parameter $h \in [0, 0.16]$ on the infectious states for the ODE model. Initial conditions are the same as in Fig. 2 and the parameter values used are as given in Table 1 with $g = 0$ and $\beta_{aa} = 0.3$ for **a–c**, and $\beta_{aa} = 0$ for **d–f**

$$
\begin{cases}
c_5 &= -\beta_{bm}(1-\epsilon)S_m^*\beta_{ma}\epsilon\beta_{aa}^2,\\
c_4 &= \beta_{bm}(1-\epsilon)S_m^*\beta_{aa}\left\{\beta_{aa}A_3+2\beta_{ma}\epsilon A_2\right\}\\
&\quad -\beta_{aa}\beta_{am}\epsilon\frac{S_m^*}{S_a^*}\left\{\sigma\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon A_1\right\},\\
c_3 &= \beta_{aa}\beta_{am}\epsilon\frac{S_m^*}{S_a^*}\left\{A_1A_3\right.\\
&\quad +\beta_{bm}(1-\epsilon)\big(h(1-\epsilon)+g\epsilon+\mu_m\big)S_m^*\\
&\quad \left.-\beta_{mb}(1-\epsilon)S_b^*(h+\nu_b)\right\}-\beta_{ma}\epsilon\beta_{bm}(1-\epsilon)S_m^*A_2^2\\
&\quad +\beta_{am}\epsilon\frac{S_m^*}{S_a^*}A_2\left\{\sigma\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon A_1\right\}\\
&\quad -2\beta_{aa}\beta_{bm}(1-\epsilon)S_m^*\left\{A_2A_3+\beta_{ma}\epsilon(\mu_a+\nu_a)\right\},\\
c_2 &= +2\beta_{bm}(1-\epsilon)S_m^*(\mu_a+\nu_a)\left\{\beta_{aa}A_3+\beta_{ma}\epsilon A_2\right\}\\
&\quad +\beta_{bm}(1-\epsilon)S_m^*A_3A_2^2+\beta_{am}\epsilon\\
&\quad \frac{S_m^*}{S_a^*}A_2\left\{\beta_{mb}(1-\epsilon)S_b^*\big(h+\nu_b\big)-A_1A_3\right\}\\
&\quad +\big(h(1-\epsilon)+g\epsilon+\mu_m\big)\beta_{am}\epsilon\frac{S_m^*}{S_a^*}\left\{\beta_{am}\epsilon\right.\\
&\quad \left.\frac{S_m^*}{S_a^*}A_1-\beta_{bm}(1-\epsilon)S_m^*A_2\right\}\\
&\quad -\beta_{am}\epsilon\frac{S_m^*}{S_a^*}(\mu_a+\nu_a)\left\{\sigma\beta_{mb}(1-\epsilon)S_b^*+\beta_{ma}\epsilon A_1\right\},\\
c_1 &= \beta_{am}\epsilon\frac{S_m^*}{S_a^*}(\mu_a+\nu_a)\\
&\quad \left\{A_1A_3+\beta_{bm}(1-\epsilon)\big(h(1-\epsilon)+g\epsilon+\mu_m\big)S_m^*\right.\\
&\quad \left.-\beta_{mb}(1-\epsilon)S_b^*(h+\nu_b)\right\}\\
&\quad -\beta_{bm}(1-\epsilon)S_m^*(\mu_a+\nu_a)\\
&\quad \left\{2A_2A_3+\beta_{ma}\epsilon(\mu_a+\nu_a)\right\}.\\
C_0 &= \beta_{bm}(1-\epsilon)S_m^*A_3(\mu_a+\nu_a)^2.
\end{cases}
\tag{2.15}
$$

The probability of extinction can be determined from (2.11) using (2.13) and (2.14). However, a simple analytical expression for $\mathbb{P}_0$ cannot easily be obtained; in the next section, it is determined numerically.

Results

To determine the effects of *Varroa*-sensitive hygienic and/or grooming behaviours on the probability of extinction or outbreak of DWV in a honeybee colony, the following cases are considered:

(i) Colonies with bee-to-bee transmission of DWV ($\beta_{aa} \neq 0$).

(ii) Colonies without bee-to-bee transmission of DWV ($\beta_{aa} = 0$).

Considering case (*i*) and the parameter values in Table 1, leads to $\rho(\mathbb{E}) = 1.6$. The fixed point (0.5871,0.2664,0.0214) calculated from (2.13) and (2.14) is used to determine $\mathbb{P}_0$. Considering case (ii) results in $\rho(\mathbb{E}) = 1.2$, and the fixed point (0.7507,0.0354,0.0354), which is used to calculate $\mathbb{P}_0$. The probability of virus extinction based on the above cases and the initial conditions $I_b(0) = i_b$, $I_a(0) = i_a$, and $I_m(0) = i_m$ is given in Table 3.

From Table 3, considering case (*i*), there is a slightly large probability of virus extinction ($\mathbb{P}_0 > 0.5$) when the virus is initiated by an infected pupa, but when it is initiated by an adult bee and a mite, respectively, the probability is small ($\mathbb{P}_0 < 0.3$) and very small ($\mathbb{P}_0 < 0.03$).

Considering case (*ii*), there is a large ($\mathbb{P}_0 > 0.7$) and a very large ($\mathbb{P}_0 > 0.9$) probability when the virus emerges from the pupa and adult bee populations, respectively. When it starts in the mite population, the probability is very small ($\mathbb{P}_0 < 0.04$) like in the previous case.

In both cases, the probability decreases with increasing initial conditions, and it falls to its lowest value when there is at least one infectious individual in each group at the beginning of an outbreak.

Some sample paths for the initial conditions (1,0,0), (0,1,0), and (0,0,1) in Table 3 are graphed in Fig. 2 with the ODE solutions. When the virus is initiated by an adult bee or a mite, sample paths of the CTMC can persist; when the virus originates from pupae, the corresponding sample path

Table 5 Effects of grooming behaviour on the probability of extinction calculated from the branching process

			(*i*)			(*ii*)		
Initial conditions			$\mathbb{P}_0$ ($\beta_{aa} = 0.3$)			$\mathbb{P}_0$ ($\beta_{aa} = 0$)		
i_b	i_a	i_m	$g = 0$	$g = 0.075$	$g = 0.15$	$g = 0$	$g = 0.075$	$g = 0.15$
1	0	0	0.5871	0.6431	0.6752	0.7507	0.8252	0.8697
0	1	0	0.2664	0.2665	0.2665	0.9969	0.9980	0.9986
0	0	1	0.0214	0.0366	0.0528	0.0354	0.0730	0.1237

The parameter values used are as given in Table 1 with $h = 0$ and $g \in [0, 0.15]$

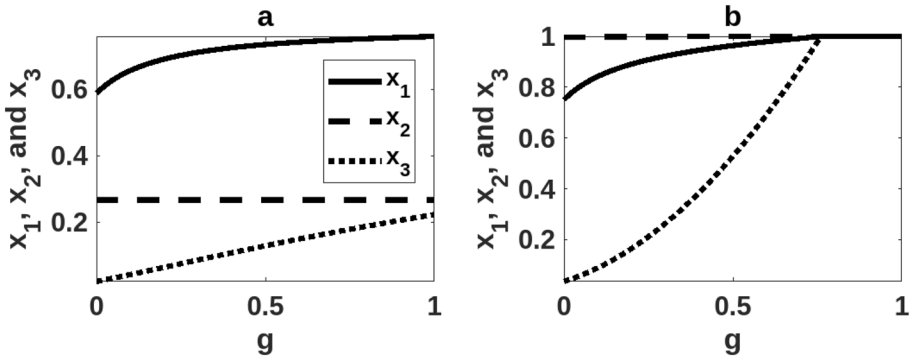

Fig. 5 Effects of grooming behaviour on the probabilities of virus extinction x_1, x_2, and x_3 in pupae, adult bees, and mites, respectively. The parameter values used are as given in Table 1 with $g \in [0, 1]$, $h = 0$, $\beta_{aa} = 0.3$ for **a**, and $\beta_{aa} = 0$ for **b**

is absorbed. On the other hand, the trajectories of the ODE model persist for all infectious individuals. The figure illustrates one of the key differences between CTMC and ODE models when the basic reproduction number ($\mathcal{R}_0$) is greater than unity; that is, the CTMC model predicts either virus extinction or persistence, whereas the ODE model predicts only persistence.

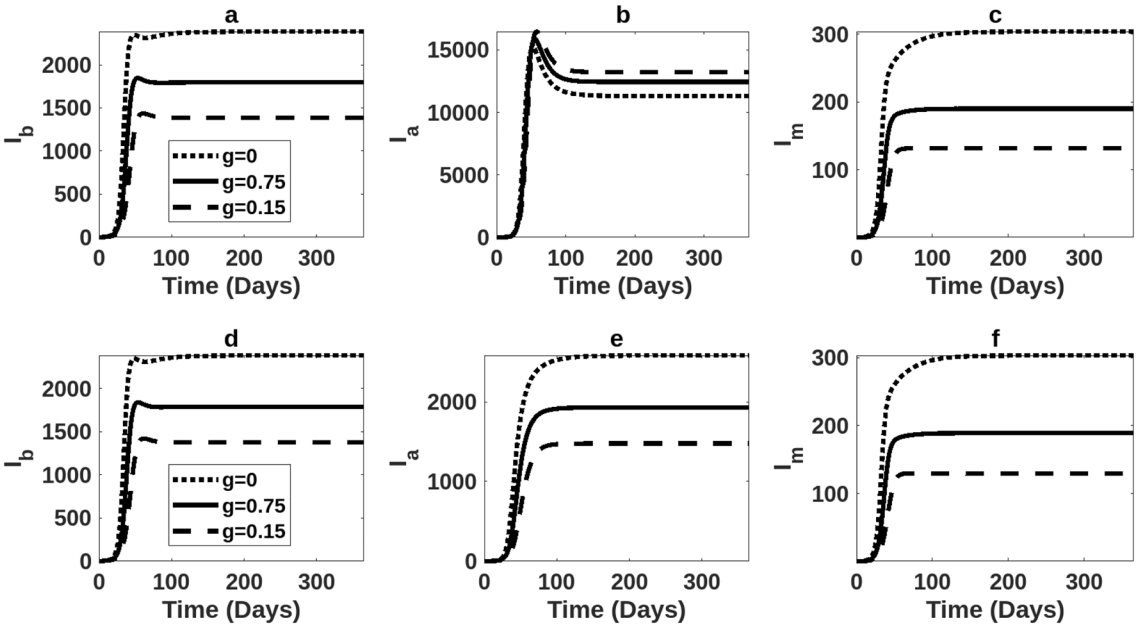

Fig. 6 Effects of varying the grooming behaviour parameter $g \in [0, 0.15]$ on the infectious states for the ODE model. Initial conditions are the same as in Fig. 2 and the parameter values used are as given in Table 1 with $h = 0$ and $\beta_{aa} = 0.3$ for **a-c**, and $\beta_{aa} = 0$ for **d-f**

Table 6 Effects of *Varroa*-sensitive hygienic and grooming behaviours on the probability of extinction calculated from the branching process

			(*i*)			(*ii*)		
Initial conditions			$\mathbb{P}_0$ ($\beta_{aa} = 0.3$)			$\mathbb{P}_0$ ($\beta_{aa} = 0$)		
i_b	i_a	i_m	$h = 0$	$h = 0.08$	$h = 0.16$	$h = 0$	$h = 0.08$	$h = 0.16$
			$g = 0$	$g = 0.075$	$g = 0.15$	$g = 0$	$g = 0.075$	$h = 0.15$
1	0	0	0.5871	0.7781	0.8427	0.7507	0.9723	1.0000
0	1	0	0.2664	0.2665	0.2667	0.9969	0.9993	1.0000
0	0	1	0.0214	0.1942	0.4475	0.0354	0.6695	1.0000

The parameter values used are as given in Table 1 with $h \in [0, 0.16]$ and $g \in [0, 0.15]$

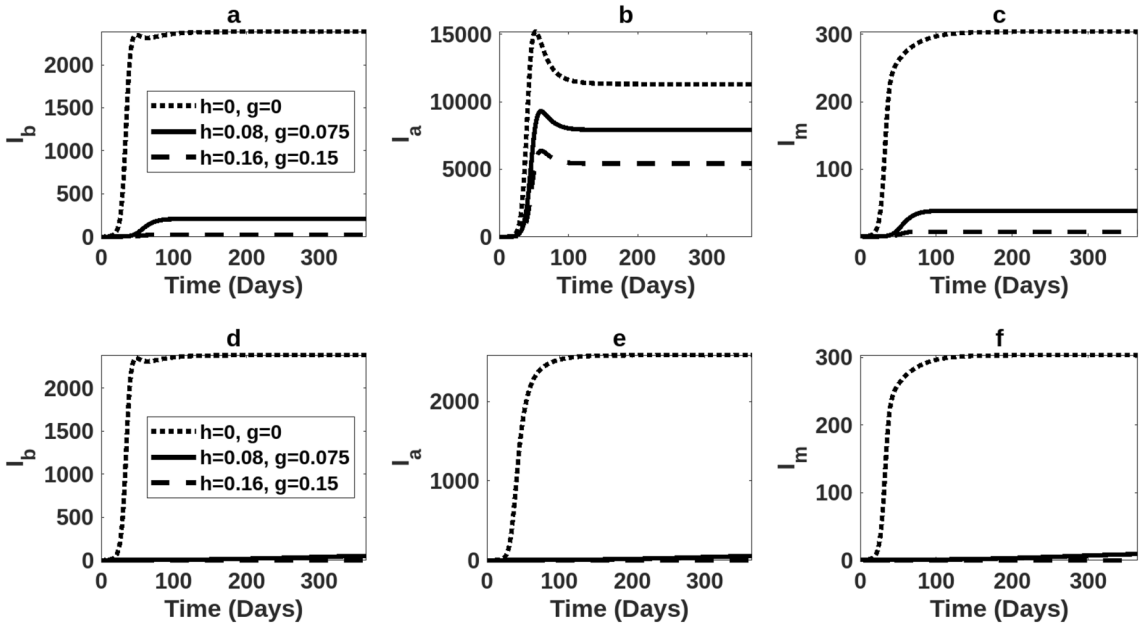

Fig. 7 Effects of varying both the hygienic and grooming behaviour parameters $h, g \in [0, 0.4]$ on the infectious states for the ODE model. Initial conditions are the same as in Fig. 2 and the parameter values used are as given in Table 1 with $\beta_{aa} = 0.3$ for **a-c**, and $\beta_{aa} = 0$ for **d–f**

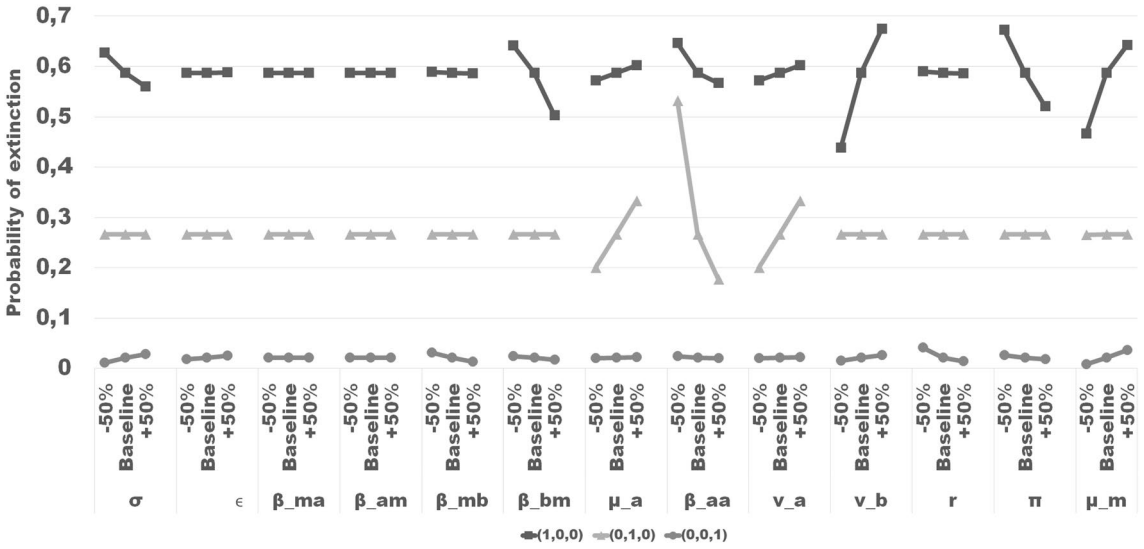

Fig. 8 Illustration of the values given in Tables 7–12 representing the effects of parameter variations on the probability of virus extinction

Effects of *Varroa*-sensitive hygienic behaviour

The effects of varying the *Varroa*-sensitive hygienic parameter (h) on the probability of the virus extinction are studied in Table 4. According to Santos (de Figueiró et al. 2016), $h \in [0.08, 0.4]$. We choose $h = 8\%$, a case for European species, and $h = 16\%$ a case for African or Asian species. To get a clear picture of how $\mathbb{P}_0$ varies with h, the individual probabilities of virus extinction x_1, x_2 and x_3, in pupae, adult bees, and mite populations, respectively, are illustrated in Fig. 3 for $h \in [0, 1]$.

From Table 4 and Fig. 3, increasing the value of the *Varroa*-sensitive hygienic parameter increases the probability of extinction. When the virus originates from the pupa population, increasing the value of h results in significantly large values of $\mathbb{P}_0$, whether there is bee-to-bee (case (i)) or no bee-to-bee (case (ii)) transmission. When the virus is initiated by a mite, increasing h can result in the extinction of the virus. The values of $h > 20\%$ and $h > 8\%$ are required to cause

an extinction for case (*i*) (Fig. 3**a**) and case (*ii*) (Fig. 3**b**), respectively. When the virus starts in adult bees, increasing h has a negligible effect on $\mathbb{P}_0$ for case (*i*) (Fig. 3**a**) and a very large effect for case (*ii*) (Fig. 3**b**).

The results in Table 4 are confirmed by simulations of the ODE model depicted in Fig. 4. When there is bee-to-bee transmission, the infectious populations decrease as h increases, but the virus persists in both populations (Fig. 4a–c). When there is no bee-to-bee transmission, the trajectories of infectious populations decrease to zero for $h = 0.16$ (Fig. 4 d–f).

Effects of grooming behaviour

To determine the effects of grooming behaviour on the probability of DWV extinction or outbreak, $\mathbb{P}_0$ is calculated at different values of g and the results are summarised in Table 5. We choose $g \in [0, 0.15]$ as used by the authors in Torres and Torres (2020). In the literature, large values of g are observed. For instance, Peng et al. (1987) reports a grooming rate of 73.8%, Rosenkranz et al. (1997) found a value of 45% and in Moretto et al. (1991) the value of 38.5% is observed. Thus, in Fig. 5 the effects of such large values on x_1, x_2, and x_3 are illustrated.

From Table 5 and Fig. 5, increasing the grooming rate parameter results in an increase in the probability of virus extinction. For case (*i*), increase in g results in a significant increase in $\mathbb{P}_0$ only when the virus is initiated by a pupa. When it is initiated by a mite or an adult bee, $\mathbb{P}_0 < 0.3$ for all values of g. For case (*ii*), increase in g results in a significant increase in $\mathbb{P}_0$ in all populations. When the virus is initiated by a mite, large values of $g \geqslant 45\%$ are required to increase $\mathbb{P}_0$ to values greater than 0.5. In fact, values of $g \geqslant 70\%$ can result in $\mathbb{P}_0 = 1$.

Solutions of the ODE model (2.1) illustrating the effects of increasing the grooming rate parameter $g \in [0, 0.15]$ are depicted in Fig. 6. For both cases, there is a reduction in infectious cases, but the virus persists with large numbers in all populations, especially in adult bees.

Combined effects of *Varroa*-sensitive hygienic and grooming behaviours

Species such as the South African Cape honeybee (*Apis mellifera capensis*) and the African savannah honeybee (*Apis mellifera scutellata*) are effective at both grooming and hygienic behaviours (Nganso et al. 2017). It is interesting to know if an outbreak can occur in colonies containing such species of bees. Thus, the effects of both *Varroa*-sensitive hygienic and grooming behaviours on the probability of virus extinction are explored in Table 6.

From Table 6, considering case (*i*)), a combination of h and g has a large effect on $\mathbb{P}_0$ if the virus is initiated by an infectious pupa or a mite, and a negligible effect if it is initiated by an adult bee. When case (*ii*) is considered, a very big increase in $\mathbb{P}_0$ is observed, regardless of the source of an infection. For both cases, larger values of $\mathbb{P}_0$ are observed if the behaviours are combined as compared to when they are considered individually (Tables 4 and 5).

Simulations of the ODE model for the combined effects of grooming and hygienic behaviours are depicted in Fig. 7. When a case for bee-to-bee transmission is considered, the virus persists with very small cases of infectious individuals in all populations, especially in pupae and mites (Fig. 7a–c). When a case for no bee-to-bee transmission is considered, a disease-free equilibrium point is obtained (Fig. 7d–f).

Impact of parameter variations on the probability of extinction

The true values of some model parameters given in Table 1, especially those estimated, are not known. The change in the values of those parameters could affect our results. A sensitivity analysis is used to determine the effects of variations in parameter values in Table 1 on the results of the probability of extinction given in Table 3. The probability of extinction is calculated when the baseline values of the parameters are allowed to vary by ±50%, summarised in Tables 7, 8, 9, 10, 11, 12 and depicted in Fig. 8. The strengths of $\mathbb{P}_0$ sensitivity to the parameter variations are determined by observing the slope of the lines in Fig. 8. A parameter with a negative or positive slope increases $\mathbb{P}_0$ when decreased or increased, respectively.

From Fig. 8, when the virus is introduced by an infectious pupa, the parameters with a high influence on $\mathbb{P}_0$ are the infection rate of a mite by a pupa (β_{bm}), virus-induced mortality rate of a pupa (ν_b), mite recruitment rate (π) and mite natural mortality rate (μ_m). The parameters β_{bm} and π have a negative slope, whereas ν_b and μ_m have a positive slope. When the virus is initiated by an adult bee, $\mathbb{P}_0$ is highly sensitive to the bee-to-bee transmission parameter (β_{aa}) which has a negative slope. On the other hand, when the virus is initiated by a mite, $\mathbb{P}_0$ is not overly affected by parameter variations.

Model relevance

These analyses further illustrate the importance of having both mites and virus when modelling honeybee population dynamics, as introduced by Kang et al. (2016). Including both in our stochastic model allows for all possible methods of colony death and the full range of dynamics. As seen in Fig. 2 different initial conditions result in virus extinction or a major outbreak. More importantly, by including parameters for grooming and hygienic behaviours, we were able to consider the relative importance of these behaviours.

Table 7 Effects of increasing or decreasing the baseline values of σ and ϵ by 50% on the probability of extinction ($\mathbb{P}_0$) calculated from the branching process. Other parameter values are as given in Table 1 with $h = 0$ and $g = 0$

			(i)	(ii)	(iii)
Initial			50% decrease	Baseline	50% increase
conditions			($\sigma = 0.04$)	($\sigma = 0.08$)	($\sigma = 0.12$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.6268	0.5871	0.5597
0	1	0	0.2664	0.2664	0.2664
0	0	1	0.0115	0.0214	0.0285
			(iv)	(v)	(vi)
Initial			50% decrease	Baseline	50% increase
conditions			($\epsilon = 0.125$)	($\epsilon = 0.25$)	($\epsilon = 0.375$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5867	0.5871	0.5877
0	1	0	0.2664	0.2664	0.2664
0	0	1	0.0184	0.0214	0.0255

Also, the combination of these behaviours leads to larger probabilities of virus extinction and faster convergence of trajectories. The numerical solutions of the ODE version of the model agree with the stochastic dynamics. Overall, the model as given is minimally required to consider the effects of these behaviours on honeybee colony survival rates.

Discussion

Large losses of honeybee colonies cause significant economic losses to crop farmers and the apiculture sector worldwide. *Varroa destructor* mites and the viruses they spread, especially the deformed wing virus (DWV), have been implicated as the main causes of these losses (Rosenkranz et al. 2010; Martin et al. 1998; Underwood and López-Uribe 2019). The Asian honeybee (*Apis cerana*) and African subspecies of *Apis mellifera* have natural resistance mechanisms: the use of grooming and hygienic behaviours against mites (Fries et al. 1996; Nganso et al. 2017). A clear understanding of the effects of these behaviours on the mites and the viruses they transmit can be important in reducing the losses of honeybee colonies. The effects of these mechanisms on the population of *Varroa* mites have been studied by several authors (Russo et al. 2020; Fries et al. 1996; Nganso et al. 2017; de Figueiró et al. 2016; Pritchard 2016; Torres and Torres 2020). In this study, a stochastic model was formulated using the assumptions of an ordinary differential equation model of the system similar to that used by Kang et al. (2016) but including parameters for grooming and hygienic behaviours.

This stochastic model was used to determine the impacts of these behaviours on the probability of extinction or outbreak of DWV in honeybee colonies infested by *V. destructor*. The probability of virus extinction ($\mathbb{P}_0$, see (2.11)) was determined using branching process theory by approximating the model near the disease-free equilibrium. The stochastic model developed here is minimally required to investigate the effects of these control behaviours on honeybee colony survival rate. The numerical solutions of the original ODE model compare well to stochastic dynamics, and the effects of the behaviours are realistic.

The probability of extinction was calculated considering two situations: when there is bee-to-bee and when there is no bee-to-bee transmission. For bee-to-bee transmission, there is a large probability of extinction ($\mathbb{P}_0 < 0.3$) when the virus is initiated by a pupa and a very small probability when it is initiated by an adult bee or a mite ($\mathbb{P}_0 < 0.03$). However, it should be noted that it is unclear whether bee-to-bee transmission of DWV occurs (Mockel et al. 2011). For cases where there is no bee-to-bee transmission, the probability of extinction is small ($\mathbb{P}_0 < 0.04$) only when the virus is initiated by mites, which indicates that vectorial transmission by mites is the primary cause of DWV outbreaks in honeybee colonies. Therefore, control or management activities that directly target the population of mites or keep them away from the hives can greatly reduce the chances of DWV outbreaks.

These results depend on the initial conditions, with the probability of extinction dropping with larger initial numbers. Thus, regular inspections are necessary to detect mites and the virus early enough before the numbers of infectious individuals are large enough to cause a major outbreak. For

example, vertical transmission can occur through the queen mating with an infectious drone (Mockel et al. 2011). This transmission could result in an outbreak of DWV if a large number of eggs hatch into infected pupae.

To study the effects of *Varroa*-sensitive hygienic behaviour, the probability of virus extinctions is determined for different values of the hygienic rate parameter (h). Increasing the value of h results in an increase in the values of $\mathbb{P}_0$. This result is confirmed by solutions of the ODE model (2.1) with a reduction in the infectious cases when h is increased. With bee-to-bee transmission, large probabilities of extinction ($\mathbb{P}_0 > 0.5$) are obtained when the virus is initiated by a pupa or a mite with high hygienic behaviour in the colony ($h > 20\%$). Smaller extinction rates ($\mathbb{P}_0 < 0.3$) are obtained when it is initiated by an adult bee. In the case of no bee-to-bee transmission, large probabilities of extinction are obtained in all populations when there is a high degree of hygienic behaviour ($h > 8\%$). Also, in this situation, the trajectories of the ODE model approach a disease-free equilibrium point. These results imply that hygienic bees can prevent an outbreak of DWV if there is no transmission between adult bees. Thus, *Apis cerana*, an example of hygienic bees (able to remove approximately 32% of the mite-infested brood (Vandame et al. 2000)), are more likely to prevent an outbreak of DWV through hygienic behaviour, especially if there is no bee-to-be transmission. On the other hand, *Apis mellifera* which are only able to remove around 8% of the mite-infested brood (Vandame et al. 2000), are less likely to prevent an outbreak through hygienic behaviour.

To study the impacts of grooming behaviour, the probability of virus extinction is considered for different levels of grooming (g). With bee-to-bee transmission, an increase in g results in significant increases in the probability of virus extinctions, but only when the virus is initiated by a pupa. The increase is insignificant when it is initiated by a mite or an adult bee ($\mathbb{P}_0 < 0.3$ for all values of g). This indicates that grooming behaviour cannot stop an outbreak of DWV if transmission between adult bees takes place. When there is no bee-to-bee transmission, an increase in g results in a significant increase in the probability of virus extinction in all populations. However, if the virus originates in the mite population, values of $g \geqslant 45\%$ are required to increase $\mathbb{P}_0$ to values greater than 0.5. Large grooming rate values of 45% and 73.8% for *Apis cerana* honeybees have been reported in the studies by Peng et al. (1987) and Rosenkranz et al. (1997), respectively. Such large values indicate that bees that are highly effective at grooming can prevent an outbreak of DWV in colonies where transmission between adult bees does not occur. In a colony, large values of g can be obtained by sugar dusting the bees to stimulate their grooming behaviour (Underwood and López-Uribe 2019).

In comparison to each individual behaviour, a combination of grooming and hygienic behaviours increases the probability of virus extinction more than a single behaviour. Also, this combination results in faster convergence of the trajectories of the ODE model to a disease-free equilibrium. Thus, species such as the South African Cape honeybee (*Apis mellifera capensis*) and the African savannah honeybee (*Apis mellifera scutellata*), which are effective at both grooming and hygienic behaviours (Nganso et al. 2017), have a greater probability of preventing a major outbreak than those that are effective at only one behaviour. Therefore, when selecting colonies for breeding, beekeepers should target those that demonstrate both grooming and hygienic behaviours.

Table 8 Effects of increasing or decreasing the baseline values of β_{ma} and β_{am} by 50% on the probability of extinction ($\mathbb{P}_0$) calculated from the branching process. Other parameter values are as given in Table 1 with $h = 0$ and $g = 0$

			(i)	(ii)	(iii)
Initial			50% decrease	Baseline	50% increase
conditions			($\beta_{ma} = 0.06$)	($\beta_{ma} = 0.12$)	($\beta_{ma} = 0.18$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5871	0.5871	0.5871
0	1	0	0.2664	0.2664	0.2664
0	0	1	0.0215	0.0214	0.0214
			(iv)	(v)	(vi)
Initial			50% decrease	Baseline	50% increase
conditions			($\beta_{am} = 0.06$)	($\beta_{am} = 0.12$)	($\beta_{am} = 0.18$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5872	0.5871	0.5871
0	1	0	0.2665	0.2664	0.2664
0	0	1	0.0214	0.0214	0.0214

Table 9 Effects of increasing or decreasing the baseline values of β_{mb} and β_{bm} by 50% on the probability of extinction ($\mathbb{P}_0$) calculated from the branching process. Other parameter values are as given in Table 1 with $h = 0$ and $g = 0$

			(i)	(ii)	(iii)
Initial			50% decrease	Baseline	50% increase
conditions			($\beta_{mb} = 0.0002$)	($\beta_{mb} = 0.0003$)	($\beta_{mb} = 0.0005$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5887	0.5871	0.5858
0	1	0	0.2664	0.2664	0.2664
0	0	1	0.0317	0.0214	0.0130
			(iv)	(v)	(vi)
Initial			50% decrease	Baseline	50% increase
conditions			($\beta_{bm} = 0.0002$)	($\beta_{bm} = 0.0003$)	($\beta_{bm} = 0.0005$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.6412	0.5871	0.5022
0	1	0	0.2664	0.2664	0.2664
0	0	1	0.0245	0.0214	0.0178

Table 10 Effects of increasing or decreasing the baseline values of μ_a and β_{aa} by 50% on the probability of extinction ($\mathbb{P}_0$) calculated from the branching process. Other parameter values are as given in Table 1 with $h = 0$ and $g = 0$

			(i)	(ii)	(iii)
Initial			50% decrease	Baseline	50% increase
conditions			($\mu_a = 0.02$)	($\mu_a = 0.04$)	($\mu_a = 0.06$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5724	0.5871	0.6018
0	1	0	0.1999	0.2664	0.3327
0	0	1	0.0207	0.0214	0.0222
			(iv)	(v)	(vi)
Initial			50% decrease	Baseline	50% increase
conditions			($\beta_{aa} = 0.15$)	($\beta_{aa} = 0.3$)	($\beta_{aa} = 0.45$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.6461	0.5871	0.5674
0	1	0	0.5314	0.2664	0.1776
0	0	1	0.0249	0.0214	0.0204

An analysis was also performed to assess the sensitivity of extinction probabilities to parameter variations. The parameters with the highest influence are the bee-to-bee transmission rate (β_{aa}), the mortality rate of pupa (ν_b), mite recruitment (π) and mortality (μ_m) rates, and the pupa-to-mite transmission rate (β_{bm}). The parameters β_{bm}, π, and β_{bm} have a negative slope, which implies that they should be reduced so as to minimise the chances of the virus outbreak. Control measures that limit direct contact between infected and susceptible adult bees, such as stocking bees from healthy hives and regular re-queening to ensure strong and healthy hives, can reduce β_{aa}. The parameters π and β_{bm} can all be decreased by keeping highly hygienic bees, such as Asian and African honeybees, and limiting mite reproduction, as discussed in Underwood and López-Uribe (2019). On the other hand, ν_b and μ_m have a positive slope, which indicates that they should be increased in order to avoid outbreaks of DWV in honeybee colonies. Keeping hygienic

Table 11 Effects of increasing or decreasing the baseline values of ν_a and ν_b by 50% on the probability of extinction ($\mathbb{P}_0$) calculated from the branching process. Other parameter values are as given in Table 1 with $h = 0$ and $g = 0$

			(i)	(ii)	(iii)
Initial			50% decrease	Baseline	50% increase
conditions			($\nu_a = 0.02$)	($\nu_a = 0.04$)	($\nu_a = 0.06$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5723	0.5871	0.6019
0	1	0	0.1998	0.2664	0.3329
0	0	1	0.0207	0.0214	0.0222
			(iv)	(v)	(vi)
Initial			50% decrease	Baseline	50% increase
conditions			($\nu_b = 0.1$)	($\nu_b = 0.2$)	($\nu_b = 0.3$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.4380	0.5871	0.6742
0	1	0	0.2664	0.2664	0.2664
0	0	1	0.0159	0.0214	0.0269

Table 12 Effects of increasing or decreasing the baseline values of r, π, and μ_m by 50% on the probability of extinction ($\mathbb{P}_0$) calculated from the branching process. Other parameter values are as given in Table 1 with $h = 0$ and $g = 0$

			(i)	(ii)	(iii)
Initial conditions			50% decrease	Baseline	50% increase
			($r = 750$)	($r = 1500$)	($r = 2250$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.5901	0.5871	0.5861
0	1	0	0.2661	0.2664	0.2665
0	0	1	0.0417	0.0214	0.0144
			(iv)	(v)	(vi)
Initial conditions			50% decrease	Baseline	50% increase
			($\pi = 6$)	($\pi = 12$)	($\pi = 18$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.6721	0.5871	0.5210
0	1	0	0.2665	0.2664	0.2662
0	0	1	0.0267	0.0214	0.0185
			(vii)	(v)	(viii)
Initial conditions			50% decrease	Baseline	50% increase
			($\mu_m = 0.02$)	($\mu_m = 0.04$)	($\mu_m = 0.06$)
i_b	i_a	i_m	$\mathbb{P}_0$	$\mathbb{P}_0$	$\mathbb{P}_0$
1	0	0	0.4667	0.5871	0.6426
0	1	0	0.2660	0.2664	0.2665
0	0	1	0.0084	0.0214	0.0364

bees and fostering the grooming behaviour of adult bees by sugar dusting can increase ν_b and μ_m, respectively.

In the most probable case, when bee-to-bee transmission does not play a major role (Mockel et al. 2011), conclusions suggested from this study are:

(i) hygienic behaviour is very likely to stop an outbreak of DWV in honeybee mite-infested colonies.

(ii) grooming behaviour is less likely to control an outbreak unless it occurs at a very high rate ($g \geqslant 45\%$).

(iii) honeybees that practice both grooming and hygienic behaviours, even at low rates, have a large probability of preventing a major outbreak.

(iv) there is a small probability of extinction if the virus emerges from the mites or adult bees, and as such, a control programme that targets both mites and bees can yield better results.

(v) the management activities for the control of the virus can be effective if they are implemented early enough before the numbers of infectious individuals are large enough to cause an outbreak.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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