Dynamic modelling of honey bee (*Apis mellifera*) colony growth and failure

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ABSTRACT

Rates of honey bee colony failure have increased significantly across much of North America and Europe, which has directed attention to the need to better understand the process of bee colony growth and development, and the factors that can cause colony failure. Here we present a simple model of honey bee colony dynamics as a tool to explore what factors may have the strongest influence on colony growth and survival. Our model focuses on how internal demographic processes within a colony interact with food availability and brood rearing to alter growth trajectories. The model is implemented as a series of difference equations operating at discrete time steps to model changes in bee population day by day. We base our rate equations on the analytic models of Khoury et al. (2013), and go further by simulating colony growth across three years to capture seasonal and annual growth cycles. Our resulting model successfully captures realistic seasonal variations in colony populations. Sensitivity analysis of the model suggests that colony survival is strongly influenced by rates of forager bee mortality, food availability and factors that influence the age at which worker bees transition from working inside the hive raising brood to working outside the hive as foragers. We discuss these findings with reference to known agents that can cause colony failure. The presented model is very simple, and makes minimal assumptions, but could easily be extended to more accurately simulate the performance of field honey bee colonies and/or specific environmental or pathogen pressures.

1. Introduction

In recent years there has been widespread concern (if not alarm) over the global decline in honey bee numbers (Ratnieks and Carreck, 2010; VanEngelsdorp et al., 2009; VanEngelsdorp et al., 2010). In the UK and North America honey bee numbers have been decreasing since the 1940s (Benjamin and McCallum, 2008; Ratnieks and Carreck, 2010). This trend was accelerated by the impacts of the devastating parasitic mite *Varroa destructor*. The rate of decline increased yet further in 2006 when beekeepers in Europe and North America suffered such unusually rapid and heavy colony losses that a new term was coined to describe the phenomenon: colony collapse disorder or CCD (Ratnieks and Carreck, 2010; VanEngelsdorp et al., 2009). There is now a growing

consensus that CCD, while certainly severe, is not the result of a single new disease or causal agent, but rather is a phenomenon emerging as a result of an accumulation of varied stressors on a bee colony (Ratnieks and Carreck, 2010).

Sadly human activity has spread most of the significant bee diseases to almost all areas of the world exposing bees to unparalleled levels of pathogen stress. There is increasing evidence of sublethal pesticide doses having significant impacts on bee populations in agricultural environments (Henry et al., 2012). Climate change related factors and intensification of apicultural practices, resulting from beekeepers needing to do more with fewer operating hives, may also be contributing to the problem (Neumann and Carreck, 2010; Ratnieks and Carreck, 2010).

Modern agriculture is increasingly reliant on managed honey bee colonies to provide a pollination service for several key horticultural crops. As a consequence there is some concern that declining bee populations will impact horticultural productivity, as well as the obvious consequences for the honey industry (Aizen et al., 2009; Allen-Wardell et al., 1998). This problem has highlighted the need to better understand the factors that determine a colony's population dynamics and how they might interact to understand not only why colonies sometimes fail, but also how to best manage bee hives for optimal population growth and honey production.

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Honey bee population dynamics are unusual for a number of reasons. The total honey bee population is influenced by two discrete levels of organisation: the number of colonies in the population and the number of bees in a colony. The fates of bees sharing a colony are highly interdependent, and a colony's growth is largely determined by dynamic interactions within a colony. Each colony has just one single reproductive individual, the queen, whose sole function is to lay the eggs that develop into workers (females) and drones (males). Although workers are sterile, they work cooperatively on all colony maintenance, defence, foraging for food and brood rearing tasks. Worker honey bees are morphologically identical, but different individuals specialise on distinct and discrete behavioural roles in the colony (Seeley, 1985, 1995). The number of eggs successfully reared as larvae depends both on the population of hive bees engaged in the brood rearing tasks (nursing), and on the number of bees actively foraging to supply the colony with the floral resources (nectar and pollen) needed to raise the brood (Allen and Jeffree, 1956; Harbo, 1986; McLellan, 1978). Therefore the size of the brood population is dependent on the size of the existing adult bee population.

Lifespan and mortality of workers in a honey bee colony is also influenced by dynamic interactions between workers in the colony. The colony typically operates as a clean, hygienic, well provisioned and well-defended fortress, and consequently the mortality of bees working exclusively within the colony is very low (Dukas, 2008; Sakagami, 1968; Winston, 1987). By contrast, foraging exposes bees to high levels of metabolic stress and oxidative damage (Williams et al., 2008), as well as significant risks from predation, adverse weather and getting lost. Forager mortality rates are very high: even in a strong and healthy colony forager mortality exceeds 15% a day (Dukas, 2008; Visscher and Dukas, 1997; Woyciechowski and Moron, 2009). A bee's total lifespan is, therefore, influenced by the age at which it commences foraging, and this factor is determined by mechanisms of social feedback within a colony. The age at which a bee becomes a forager is governed by a pheromone-mediated system of social inhibition (Huang and Robinson, 1999; Leoncini, 2004). Foragers produce a pheromone, ethyl oleate, which they transfer to hive bees by oral food exchange (trophallaxis) (Leoncini, 2004). This delays the rate at which hive bees become foragers. If there is a superabundance of existing foragers in the population, recruitment of new foragers is delayed, but if the forager population is diminished recruitment of new foragers is accelerated (Huang and Robinson, 1996). In effect there is a negative feedback between the proportion of existing foragers in the colony and the rate at which younger hive bees enter the foraging pool, with the result that the colony maintains a relatively stable ratio of hive bees to forager bees (Huang and Robinson, 1999).

Previously, Khoury et al. (2011) developed a compartment model using simple differential equations to mathematically describe the colony population dynamics and explore the causes of colony failure. This model was later further developed to explicitly model the dynamics of brood rearing and food flow in the colony (Khoury et al., 2013). Exploration of the models suggested that there was a critical threshold of forager death rate, which if exceeded would drive a colony to rapid depopulation and death (Khoury et al., 2011, 2013).

These models were highly simplified approaches to colony demographics: their purpose was to explore possible interactions between factors rather than to explicitly simulate the reality of colonies. Because of the structure of a compartment model these were unable to consider the effects of the variation of many of the key parameters known to influence colony growth and mortality over a seasonal cycle, such as food availability, queen laying rate and forager mortality. To create a more realistic simulation of how a honey bee colony population would be expected to change with time and across seasons, we translated the equations from Khoury et al. (2013) to a dynamic flow model using difference equations implemented at discrete time steps, to model sequential changes in bee population day by day. Our intention was to develop a model structure that, while still operating under minimal assumptions, allowed exploration of how internal social dynamics and external seasonal variables might interact to determine seasonal colony population cycles.

2. Constructing the model

The dynamic model is based on the mathematical models of Khoury et al. (2011, 2013). Following Khoury et al. (2013) our model only considers the population of female worker bees, since the male drones make no contribution to colony work and are effectively parasitic on the colony. According to Jay (1974), no more than 5% of brood become drones.

Worker bees were divided into two discrete populations: hive bees that operate within the hive raising brood, and foragers that operate outside the hive gathering food and materials for the colony (principally pollen and nectar). These are distinct behavioural castes (Seeley, 1985, 1995; Winston, 1987), which we treat as mutually exclusive. Worker bees enter the population from eggs laid by the queen. They hatch into larval brood which are fed intensively by hive bees before being sealed into their cells and entering the pupal stage. During this time they require no feeding and metamorphose into adult bees after nearly two weeks (Winston, 1987). We assume that brood survival is dependent on the number of hive bees available to tend and feed brood, on food availability and on the laying rate of the queen. We assume that brood emerges as adult bees at a constant rate proportional to the number of pupae present. Adult worker bees initially work as hive bees, and become foragers when they are older (Winston, 1987). The age at which hive bees become foragers is influenced by the number of forager bees already present in the colony (Beshers et al., 2001; Huang and Robinson, 1996, 1999; Leoncini, 2004; Robinson et al., 1994). Any factor causing depletion of the colony foraging force reduces the strength of social inhibition, resulting in a precocious (i.e. early) onset of foraging behaviour in hive bees (Huang and Robinson, 1996). Once bees have adopted the foraging role they usually maintain that function until they die, however under extreme conditions that deplete the population of nurse bees, foragers can 'revert' to hive bees (Huang and Robinson, 1999). Under most conditions the death rate of hive bees is low, but the death rate of forager bees is relatively high. On average bees survive less than one week of foraging (Woyciechowski and Moron, 2009).

Here we have implemented the equations and the initial conditions from Khoury et al. (2013) in a dynamic flow model using difference equations implemented at discrete time steps, each of one day duration. This allowed us to incorporate seasonal factors into a time-based model of how colony populations would change across several years.

2.1. Model implementation

A dynamic flow model was constructed using the Stella software (isee systems, Version 8.0). The model, illustrated in Fig. 1, calculates the changes in the population of bees over a three year period under the influence of initial conditions, food availability and varying death rates.

Queen-laid eggs enter the system at a particular laying rate, hatch to become larvae after three days, and are sealed into cells as pupae after a further five days. The pupae emerge as adult hive bees, in a process called eclosion, after a further twelve days (Fukuda and Sakagami, 1968; Garofalo, 1977). Hive bees transition into forager bees at a particular rate, or as discussed in a previous section,
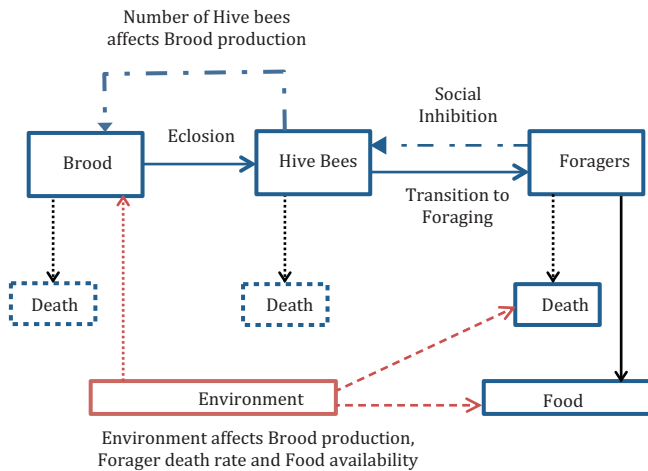
Fig. 1. The basic elements of our model of the population dynamics of honey bees. Bees enter the population as eggs which are reared as brood, passing through larva and pupal stages, before eclosing as adult hive bees after three weeks. In summer hive bees transition to forager bees after three weeks, before dying after a further week. The death rates at other stages are also considered in the model but are less significant, which is represented in the figure with dotted lines. Brood rearing is facilitated by the hive bees, so the balance between the numbers of hive bees and brood is considered in the model and represented in the figure with a dash-dot feedback arrow. Similarly, the balance between forager and hive bees is assumed in our model to be maintained through social inhibition, and illustrated here with a dash-dot feedback arrow. Foragers are the only bees in the colony with direct access to food, illustrated with a solid arrow here. The distribution of food to the rest of the colony is not shown in the figure. Finally, the environment, through the effects of seasonal variations, climate and weather affects brood production, forager bee death rates and food availability. Our model considers the seasonal variations for one particular set of weather and climate conditions, taken directly from studies in the literature.

forager bees may 'transition' backwards into hive bees under extreme conditions, as indicated by the backwards arrow in Fig. 1. All stages of the honey bee lifecycle experience some deaths, but since most deaths are usually incurred by the forager bees, this death rate is emphasised in Fig. 1.

The dynamics of food collection and consumption involve the collection of food by forager bees, and the consumption of food by adults and by the larval stage of brood production.

In this model the total period of the simulation is 36 months, where a year is divided into twelve pseudo-months, each of 30 days. Most of the data sets we have used to parameterise the model and tie to particular sets of observed conditions came from Northern Europe or North America. For this reason our model follows the Northern hemisphere seasons.

The driving equations are as follows.

The rate at which the queen bee lays eggs, L, is given by:

$$L = L_{max} \times L_s \tag{1}$$

where

L_{max} = the maximum effective egg laying rate of the queen during the year for a given population of adult bees.

L_s = the proportion of the maximum egg laying rate appropriate to the particular season.

As discussed previously, eggs turn into larvae after three days, are fed for five days, and left alone in sealed cells as pupae for twelve days (Fukuda and Sakagami, 1968; Garofalo, 1977). After each stage of brood development a certain proportion die. The newly emerged adult bees become hive bees, represented in the model by H. The transition from hive bees to forager bees (represented by F in the

model) usually takes place after about 20 days as an adult (Fukuda and Sakagami, 1968). However, the drivers governing transition are believed to depend on the relative numbers of foragers and hive bees, social inhibition and the production of pheromones.

In our model the transition rates are given by the following equations (based on Khoury et al. (2011)):

$$\frac{dH}{dT} = \text{eclosion rate} - R(H, F) \tag{2}$$

$$\frac{dF}{dT} = R(H, F) - F \times mF \tag{3}$$

where $R(H, F)$ is the rate of transition from hive bee, H, to forager, F, m_F is the forager death rate, and the *eclosion rate* is the rate of transition from the pupal stage of brood development to adult bees. In order to be consistent with the observations of Huang and Robinson (1996), Khoury et al. (2011) constructed Eq. (4) to describe the transition rate:

$$R(H, F) = \left(\frac{a - \sigma \times F}{H + F} \right) \times H \tag{4}$$

where α is a constant representing the rate of maturation of hive bees in the absence of foragers, and σ is a constant representing the effect of social inhibition on the rate of transition of hive bees to foragers. The equation reflects the experimentally demonstrated phenomenon of social inhibition in which the presence of greater numbers of forager bees in the colony inhibits the recruitment of adult bees into the foraging force (Huang and Robinson, 1996, 1999). The equation assumes that social inhibition is directly proportional to the ratio of the number of forager bees to the total number of adult bees in the colony. Clearly, if $\alpha < \sigma$ the second term in brackets can become bigger than the first term, making the rate of transition negative. This is consistent with observations that if the ratio of foragers to hive bees is high enough, forager bees revert back into hive bees (Huang and Robinson, 1996). The constants were chosen such that the minimum age at which bees can become foragers is four days old (which is the absolute youngest bees can begin foraging in the absence of social inhibition), and so that reversion only occurs when more than one third of the colony are foraging. These values were chosen to match both experimental data and the analyses of Khoury et al. (2011).

We used the extended version of this equation from Khoury (2009) to take into account the effects of a limited food supply. Eq. (5) models the effect that limited food resources has on stimulating hive bees to become foragers at a younger than normal age causing a precocious onset of foraging, as reported by Schulz et al. (1998) and Toth and Robinson (2005).

$$R(H, F, f) = \left(\frac{at - \sigma \times F}{H + F} \right) \times H \tag{5}$$

where α_t represents the effective rate of transition from hive bees to foragers in the absence of a population of foragers, which also depends on the food stored in the hive, represented by f:

$$\alpha_t = \alpha_{max} \times \left(\frac{b^2}{b^2 + f^2} \right) + \alpha_{min} \tag{6}$$

where:

α_{min} is the minimum possible transition rate, which occurs when there is plenty of food, but no foragers;

α_{max} is the maximum additional rate of transition that occurs when food stores are low; and

b is a constant that determines the steepness of the sigmoidal function that governs the rate that the food dependent term decreases as food stores increase (determined empirically so that the impact

of food shortage on recruitment was consistent with experimental observations of real colonies (Khoury, 2009)).

f is a variable describing the amount of food in a colony.

The forager bees will die at a rate given in Eq. (3), where:

$$m_F = m_s \times m_1 \tag{7}$$

The parameter m_1 is the maximum death rate of foragers in summer. However, the death rate of foragers is not observed to be constant throughout a year. In winter the lifetime of honeybees extends to many months (Mattila and Otis, 2007; Sakagami, 1968). This is modelled by adding a death rate seasonality term, m_s, which gives the proportion of the maximum death rate that is applicable throughout the year.

Food stores are modelled using the differential equation from Khoury (2009) for the rate of change of food stores, f, described by:

$$\frac{df}{dt} = cF - (\gamma_B B_L + \gamma_H H + \gamma_F F) \tag{8}$$

In the first term, c, is the food collection factor, and in the second term the brood, hive bee and forager bee food consumption rates are given by γ_B, γ_H, and γ_F, respectively. The populations are H and F for hive bees and foragers, respectively, and B_L represents the number of brood in the larval stage, the only stage of brood that consumes food.

In our model the food collection factor, c, is given by:

$$c = c_{\max} \times c_s \tag{9}$$

where: the parameter $c_{\max}$ is the highest rate at which forager bees can collect food when food is abundant. In this case, both pollen and nectar are lumped together as food. This assumption is a simplification used by (Harbo, 1993), made on the grounds that the 'value of pollen in these experiments was equal to the weight of honey (energy) used to collect it.'

The parameter c_s is the seasonality factor representing the proportion of the maximum rate of collecting food which is appropriate to the time of year for a particular location and set of environmental assumptions.

2.2. Defining functions and parameterisation

Rather than define a maximum fixed laying rate, as was done by Khoury (2009) and related papers, we chose to model the maximum effective egg laying rate, $L_{\max}$, in terms of the resulting brood which can be raised as a function of the population of adult bees (see Eq. (1)). The valuation of the parameter was determined from the results of Harbo (1986) for the number of brood raised over 19 days in June, adjusted to a daily rate, and compensated for the total losses of 15% measured by (Fukuda and Sakagami, 1968) during the brood rearing process, shown in Eq. (10).

$$L_{\max} = 402 \times \ln(H + F) - 2673 \tag{10}$$

Brood rearing is not constant throughout the year, irrespective of the population of adult bees. Brood rearing declines according to the supply of pollen (Seeley, 1985), which normally falls in autumn. However, colonies produce the same numbers of winter bees 'regardless of the timing of the disappearance of pollen resources,' (Mattila and Otis, 2007). The lifetime of autumn-reared workers is inversely proportional to the amount of brood remaining when the workers eclose. Therefore, longer lived workers only appear once brood numbers decline. Since colonies do not normally store significant pollen reserves (Blaschon et al., 1999), the seasonal changes in brood rearing should follow the seasonal changes in food collection.

The model parameter L_s represents the proportion of brood production calculated using the regression equations determined by Harbo (1986) for his experimental colonies of 9000 bees, compared with the maximum production recorded in June, as shown in Table 1.

This is modelled here using the graphical input shown in Fig. 2, which repeats in yearly cycles over three years, beginning with 1 January. The figures for those months not measured by Harbo (1986) were selected to lie between the measured months. The exact behaviour is most likely dependent upon the climatic conditions of the particular locality in question and for a particular time in history. So it is important to consider the sensitivity to changes in shape of the assumed input graph. The dip in production in August corresponds to the summer dearth, the 'period between blossoming of spring and autumnal plants' (Harbo, 1986). At this time there is abundant pollen available from grasses, but little nectar.

While Harbo (1986) recorded data at two month intervals for most of the year, there is a gap of four months over winter which may result in greater inaccuracies in our model. While the brood raising activities are expected to be low at that time of year (or entirely absent for sites far enough north geographically) the foraging activity is also likely to be low or minimal. This means that the consumption of food reserves will be sensitive to both factors at that time. The effects of these assumptions will be explored in the sensitivity analysis.

The death rates for each stage of brood rearing were taken directly from Fukuda and Sakagami (1968):

$$m_E = 5.8\%$$

$$m_L = 8.3\%$$

$$m_P = 1.5\%$$

where m_E is the egg death rate, m_L is the larva death rate, and m_P is the pupa death rate.

There is no consensus on what happens when colonies drop to a low number of adults. Ghamdi and Hoopingarner (2004) conclude that egg-laying will not occur if number of adults fall below 1000. Becher et al. (2010) and Rosenkranz (2008) conclude that heating problems lead to colony failure when adult bee numbers drop below approximately 3700, at the beginning of brood rearing after solstice. We take the critical number of adult bees to be 1500, below which the numbers of brood and adults die off at accelerated rates. The rates themselves are unknown and probably highly variable depending on specific conditions. The adults are assumed to die at rates of 0.7 for hive bees, and 0.8 for foragers. These rates are arbitrary, but are subjected to our sensitivity analysis. We assume that the queen stops laying altogether, and the egg death rate, m_E, and the larva death rate, m_L, increase to one, so that all eggs and larvae either die naturally or are cannibalised by adults. The death rate of pupae should remain unaffected in our model since they do not need to eat, and are protected from cannibalisation by being sealed in their cells. However, the outcome of assuming no effect on the death rate of pupae from low adult populations is for the eclosing pupae to boost the number of hive bees just when they are crashing. This appears to be unnatural, and seems to be an artefact of the model. There may, however, be increased deaths of pupae due to the lack of effective temperature regulation. This is handled by making the pupa death rate, m_P, equal to one when the number of hive bees drops below 1050 (which is 70% of the critical adult population of 1500). This means that once the hive bees drop below a critical population their numbers are unaffected by newly eclosing bees from pupae, whereas the numbers of pupae remaining in sealed cells drop off at the usual rate.

Similarly, if the food store parameter, f, in our model, which tracks the accumulated amount of food available to the colony in

Table 1

L_s calculations based on Harbo (1986). The row marked 'brood production' represents the calculated brood production for 9000 bees based on the regression equations derived by Harbo for each selected month. The second row in the table gives the equivalent normalised values of brood production relative to the highest value, with interpolated estimates for those months not selected by Harbo.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Brood Production		10,023		15,661		15,989		5432		8974		
Normalised brood production	0.10	0.63	0.80	0.98	0.99	1.00	1.00	0.34	0.45	0.56	0.28	0.00

the hive, drops to a low value, then we expect more dramatic death rates, whether directly from starvation, or from cannibalisation of pupae. Once the food stores drop below 100 g in our model the brood death rates are set to one, and the laying rate is set to zero. It was expected that a food store threshold of zero was an unrealistic assumption since it is likely that stress on the hive population will build up long before the food store reaches zero. These assumptions are investigated further in the sensitivity analysis.

The initial population of brood is taken to be 1000, in agreement with the observations of Seeley and Visscher (1985), with 14% eggs, 28% larvae and 58% pupae in sealed cells. Similarly, the initial populations of hive and forager adult bees are taken to be 6300 and 2700, respectively, in accord with Harbo's (1986) view of the healthiest starting colony size option.

The transition rate from hive bee to forager given by Eq. (4) is parameterised by Khoury et al. (2013) as follows:

the social inhibition constant $\sigma = 0.75$
the rate of transition when there is plenty of food, but no foragers $\alpha_{min} = 0.25$
the maximum additional rate when food stores are low $\alpha_{max} = 0.25$
the constant governing the dependence on food stores $b = 500$

The arguments supporting the choices of these values are fairly subjective, but are consistent with observations reported in the literature (Khoury, 2009). The effects of different choices of these parameters are examined further in the sensitivity analysis.

The final step in the main flow pathway is the death rate of foragers, m_F. The death rate used by Khoury (2011) was only applied to the foragers in order to be consistent with the findings of Rueppell et al. (2007), that foragers are far more likely to die than their colony-bound cousins. While this may be true in normal circumstances, it may not be true when the load of pathogens or the attack of pests becomes too high. Therefore, in this paper we consider both the death rate of foragers, m_F, and that of hive bees, m_H.

We model the death rate of forager bees using Eq. (7). The death rate seasonality parameter, m_S, shown in Fig. 3, was derived directly from the survival figures listed in Harbo (1986), as shown in Table 2. In this table the average survival figures for all populations of adult bees in a given month from Harbo were used to determine the 'average survival per 1000'. The 'equivalent death rates' that would result in the observed survival rates were calculated assuming only forager deaths, and a daily transition from hive bee to forager bee based on Eqs. (5) and (6), where food is assumed to be unlimited (as assumed by Harbo (1986)). In this case $\alpha = \alpha_{min} = 0.25$ because f is essentially infinite in Eq. (6), while $\sigma = 0.75$ as discussed previously. Finally, the 'normalised death rates' were determined as a proportion of the highest death rate, which was observed to occur in August. For those months for which there was no data in Harbo (1986), we used a simple interpolation between the two neighbouring months. The death rate for winter months was taken to be the same as for February.

We see from Table 2 that the highest average forager death rate for any month for healthy hives is about 10%. The worst possible survival rate observed by Harbo (1986) was for 36,337 bees in August, which suffered 13.4% death rate per day. Rueppell et al. (2007) found that healthy colonies of between 4500 and 9000 adult bees sustain equilibrium under forager death rates of between 11% and 16% each day. Equally, from Khoury (2011) we expect that the colony is unlikely to sustain a forager death rate of 30% each day without collapse.

Under normal circumstances the value of hive bee death rate, m_2, will be low. So for the purposes of this paper the value is
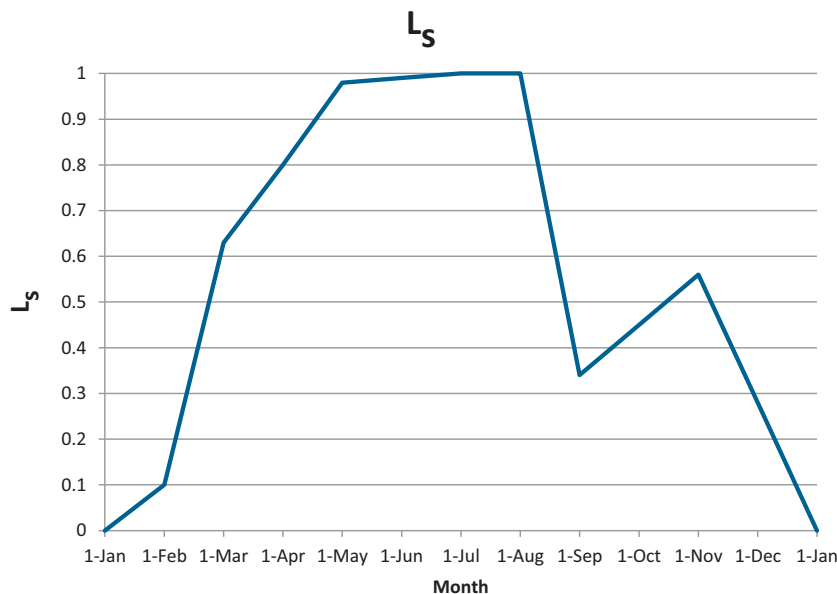

Fig. 2. Input to the model of the seasonal variation of the laying rate, L_S, over 12 months, beginning from 1 January. The pattern of laying repeats in a yearly cycle over a total of three years.
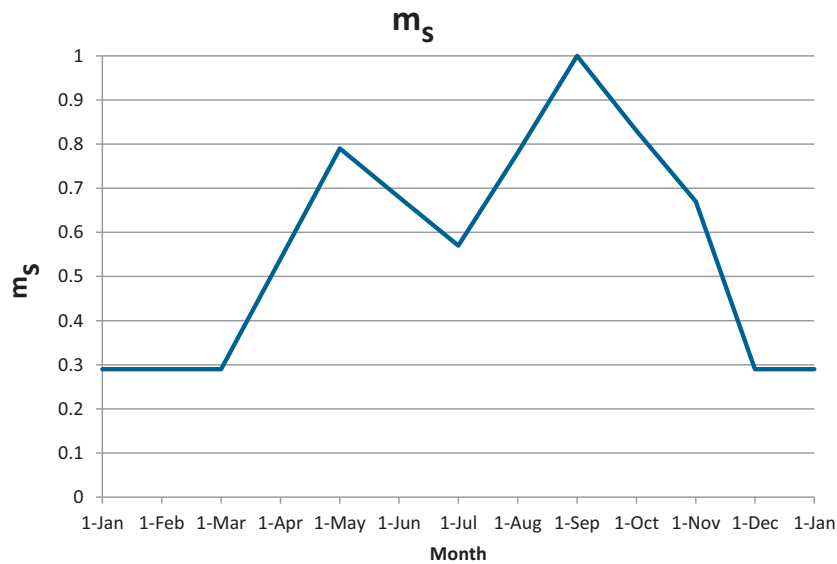
Fig. 3. Input to the model of the seasonal variation, m_S, of the forager death rate over 12 months, beginning from 1 January. The pattern repeats in a yearly cycle over a total of three years.

assumed to have a nominal value of 0.007, which is within the range found by Sakagami (1968) and Harbo (1993). However, the rate will rise under significant pathogen attack, or if the hive bee population falls below sustainable numbers.

The Food consumption rates in Eq. (8) were determined from Harbo (1993). He determined that the rate of honey consumption with no brood was 6.7 mg/bee/day for a colony with 9000 bees. He also determined that 121 g of honey was required to raise 1000 cells of mixed age brood over a period of twenty days. This translates to 6.1 mg/cell/day to raise mixed-age brood.

In order to determine seasonal food collection rates, we note that Harbo (1986) found that the greatest amount of excess food was taken in June for all populations studied. This was used to determine c_{max} in Eq. (9). Each of the June populations of adult bees was taken to be half the difference between the initial population and final population. For instance, the 9189 member colony reduced to 73% after 22 days, giving an average population over the period of 7948. Similarly, the number of brood cells was taken to be half the total counted after 19 days, or 8757 for the 9189 member colony. Therefore we estimate that the food consumed by the 9189 member colony is given by:

$$\text{Food consumed (9189 colony)} = (7948) \times 6.7 \,\text{mg/day}$$
$$+ 8757 \times 6.1 \,\text{mg/day}$$

$$\text{Food consumed (9189 colony)} = 107 \,\text{g/day}$$

Harbo (1986) determined that the "*food collection balance*" in June was +10.2 mg/bee/day for the 9189 member colony. This however, required adjustment, according to Harbo, for the weight of the brood itself. He estimated the adjustment from Nelson et al. (1924)

to be 92 mg per brood cell. This adjustment took place over 19 days, and was serviced by 7948 adult bees in our example, which equates to an added 5.3 mg/bee/day. So the adjusted food collection balance for the June 9189 member colony was +15.5 mg/bee/day.

The total food collection in June must have covered both the weight of honey increase, as well as the food consumed:

$$\text{Total food collection} = \text{Adjusted food collection balance}$$
$$+ \text{Food consumed}$$

So for our example:

$$\text{Total food collection (9189 colony)}$$
$$= +0.0155 \,\text{g/bee/day} \times 7948 + 107 \,\text{g/day}$$

$$\text{Total food collection (9189 colony)} = 230 \,\text{g/day}$$

But all food collection is carried out by foragers only. From our models we know that foragers constitute about 30% of all adults for the given population size, equating to 2384 foragers for the 9189 colony. So:

$$\text{Food collection by foragers (9189 colony)} = 230 \,\text{g}/2384/\text{day}$$

$$\text{Food collection by foragers (9189 colony)} = 97 \,\text{mg/bee/day}$$

Using the same logic for each of the June populations from Harbo (1986), omitting the lowest population (due to a failure in one of the

Table 2
Derivation of death rate seasonality. The first row shows the average survival rate per 1000 bees calculated from Table 1 of Harbo (1986) from different initial populations, for each specific month considered. The equivalent forager death rates were back calculated from the model to determine which forager death rate would result in the observed survival figures after 22 days. The last row in the table gives the equivalent normalised forager death rates relative to the highest value, with interpolated estimates for those months not selected by Harbo.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average survival per 1000		814		592		682		526		642		
Equivalent forager death rates		0.030		0.081		0.058		0.102		0.068		
Normalised death rates	0.29	0.29	0.54	0.79	0.68	0.57	0.78	1.00	0.83	0.67	0.29	0.29

Table 3
Food collected by bees through the year according to Harbo (1986). The first row shows the average food collected in terms of mg/bee/day, calculated as discussed in the text. The last row in the table gives the equivalent normalised food collection rates relative to the highest value, with interpolated estimates for those months not selected by Harbo.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Av. food collection over populations mg/bee/day		3		92		99		19		44		
Normalised food collection	0.03	0.03	0.48	0.93	0.97	1.00	0.60	0.19	0.32	0.45	0.25	0.10

trials), resulted in an average food collection over all populations in June of:

Av. Food collection by foragers (June) = 99 mg/bee/day

This provides the value for c_{max} in Eq. (9). The same calculations were carried out for the other months of the year, shown in Table 3, to determine the relative proportions of food collected compared with June. The values listed in the row 'normalised food collection' were used to determine the parameter c_s in Eq. (9) (see Fig. 4). Again, for months that were not measured by Harbo (1986) values were selected that were midway between the two neighbouring months. Some value judgement was required to select values for winter months, which are investigated in the sensitivity analysis.

The calculations in Table 3 assume that the foragers cannot bring back negative food. So when *adjusted food collection balance + food consumption* returned a negative answer for some populations (in February), the value was set to zero.

Harbo (1993) determined that it takes about 163 mg of honey to rear a worker bee to the point of pupation. Since only larvae consume food during brood rearing, a larva eats 163 mg of food in five days, at an average of 32.6 mg/day.

In our model, therefore, the total rate of honey consumption, X_f, is taken to be:

$$X_f = (F + H) \times 6.7 \text{ mg/day} + BL \times 32.6 \text{ mg/day} \quad (11)$$

3. Results

The sensitivity analysis results are presented in Table 4, which shows in the column called 'm_1 death,' the smallest value of m_1 which results in colony death (i.e. when the number of hive bees, H,

falls below 1.0) during the three year simulation, as each individual parameter is varied. In general, the relevant parameters are varied relative to the base model, shown in the column called 'Base', to the new value shown in the column called 'New', while holding the other parameters constant.

The sensitivity of the model to a change in a particular parameter shown in the column 'sensitivity,' is the percentage change in the value of 'm_1 death' compared with the base model, divided by the percentage change in the parameter compared with the base model.

In order to test the sensitivity of the 'L_S base' (the lowest laying rate in the season), a minimum laying rate of 0.1 was used as a basis for comparison, rather than zero used in the base model, to avoid a divide by zero error. Similarly, a minimum food collection seasonality factor, 'c_S base', of 0.1 was used as a basis for comparison, rather than zero used in the base model.

Not all locations experience what is called, a summer dearth in nectar flow. That is when food availability and hive activity drops in summer, and then picks up again. To investigate the impact of this we have included comparisons of c_S with and without a high value in August, and comparisons of L_S with and without a high value in August.

Another important parameter is the relative timing of different seasonalities (following Northern Hemisphere seasonal cycles). The sensitivities of the timings were assessed by changing the dates at which a parameter begins to rise from the base at the end of winter, called 'cut-in', and the time it falls to the base in autumn, called 'cut-out'. The cut-ins and cut-outs were changed by one month forwards and backwards, giving a change in parameter of 1 in 12, or 8.3%. While the outcomes depend on the precise form of the parameter curves, the results were taken as a qualitative indication of the sensitivities.
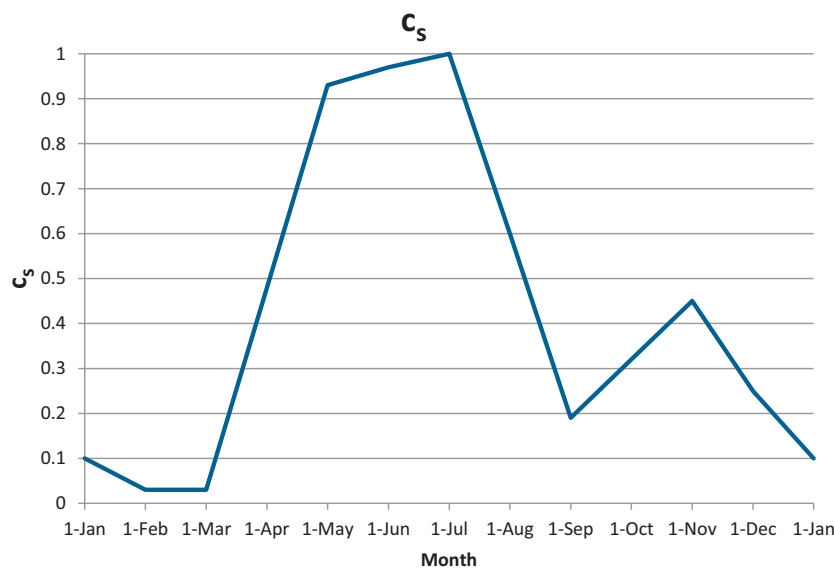

Fig. 4. Input to the model of the seasonal variation of the food collection rate, c_S, over 12 months, beginning from 1 January. The pattern repeats in a yearly cycle over a total of three years.

4. Comparing simulation model parameters to field data

Under Midwest US conditions, colony populations peak at most at 50,000 adults in the middle of July (Ghamdi and Hoopingarner, 2004). Our basic model peaks at 52,000 adults at the end of July for $m_1 = 0.1$ (see Fig. 5a). Schmickl and Crailsheim (2004) report that a honey bee colony can reach up to 75,000 individuals in a good year, with approximately 64% adult bees and 36% brood. Our basic model peaks at 82,500 individuals, with 63% adults.

Measurements of colony populations outside of summer are less frequent. DeGrandi-Hoffman et al. (1989) measured populations of $10,800 \pm 2800$ adult bees on 1 May, while Farrar (Farrar, 1934, 1936) found brood-rearing colonies contained $26,800 \pm 2700$ bees by 17 May. Avitabile (1978) reported that honey bee colonies reach a population of 30,000 by late spring. Our model, assuming $m_1 = 0.15$ (Dukas, 2008; Visscher and Dukas, 1997; Woyciechowski and Moron, 2009), gives 16,942 adults by 1 May, and 24,455 by 30 May (see Fig. 5b).

Seeley and Visscher (1985) found that the numbers of capped brood cells increase from less than 1000 capped cells in January to 30,000 capped cells by May or June. Our model with $m_1 = 0.15$ gives a minimum of 194 capped cells on 16 January, and a maximum of 16,108 on 7 August (Fig. 5b).

In our model (Fig. 5c), as the forager death rate increases up to near the critical value, we find that the Food store struggles to recover during summer, and it is clear that given enough years in the simulation the colony will eventually fail. For the critical forager death rate in our base model of $m_1 = 0.22$ (Fig. 5d), the colony finally collapses after 800 days, which corresponds to 20 March (Day 80 in the cycle). This is at the beginning of spring, when egg laying has ramped up (Fig. 2), but food collection is unable to keep up (Fig. 4). This is a critical time for bee colonies, and a common cause of collapse. If the forager death rate is increased further the colony collapses sooner in the three-year cycle of the simulation. In Fig. 5e) we model $m_1 = 0.24$, and find the colony collapses around Day 440, which again corresponds to Day 80 (20 March) in the cycle.

5. Implications of the sensitivity analysis

The base model results in starvation of the colony once the death rate is high enough. In other words, the lack of food appears to cause the colony collapse. Death by starvation is common to most combinations of parameters, and is the most common cause of colony failure in winter (Cramp, 2008). Since we are interested in the symptoms of CCD, whereby both food and pupae remain in the hive, we tracked their terminal values.

The biggest sensitivities of the model parameters from this analysis were:

- c_{max} – the m_1 death rate appears to be linearly dependant on the amount of food collected each day.
- c_S cut-in – colony survival is sensitive to when the bees start foraging early in the season.
- α – survival of the colony is inversely proportional to the strength of the inhibition to *transition* due to the current numbers of forager bees.
- c_s cut-out – the later in the season that bees can continue to harvest floral resources, the better it is for the colony survival.
- α_{min} – determines the minimum rate of *transition* from hive bees to forager bees, for the case where there are no forager bees, but plenty of food. The higher this rate of transition the more resilient the colony becomes due to the fact that there are more foragers and thus more food. There is, however, little sensitivity to parameters b or α_{max}. This means that the rate of *transition* for the case where food is limited is not an issue.

- $f(0)$ appears to be of low importance as long as the store is greater than a threshold value. However, this threshold matters because the simulation starts at mid-winter on January first, when the colony survival depends purely on food reserves, and the system has not yet achieved equilibrium. Consequently if the model begins with 5 kg of food or less, it will fail for any death rate.
- γ_F and γ_H – both food consumption factors are important, while the consumption of food by foragers is less important since their numbers are lower. As expected, the more they eat, the sooner the colony collapses due to starvation.
- m_S-cut-in – shows a moderate impact on the survival of the colony in the sense that the later the forager death rate starts to rise in the spring, the better for colony survival.
- L_s cut-out – shows that ending egg laying earlier lowers the sensitivity to colony death. This reflects the limited food resources in the colony over winter, and the need to minimise the mouths to feed.
- L_s cut-in – shows that the earlier that egg laying begins in the season, the better for colony survival. This shows that the production of more bees early in the season promotes colony survival, even in the face of the faster reduction in food reserves due to the added mouths to feed when there is little food available for foraging.

Interestingly, the sensitivity to m_2 is rather low. This suggests that the model colony is relatively robust to low levels of attack to the *Hive bee* population, including attacks from viruses, parasites and other pests and contagions, as well the effects of chemicals. However, once the rate of hive bee deaths increases enough, the model suggests that the population crashes without suffering from starvation. The only other parameter which is capable of causing colony death without starvation is when there is a low value of σ – the parameter which governs the rate of transition from hive bee to forager. According to Eqs. (4) and (5), a lower value of σ results in a higher rate of transition to foragers with a consequent enhancement in food gathering capacity.

6. Discussion

6.1. Simulation results

In essence our approach to modelling a honey bee colony is extremely simplistic. We have simply used mathematical equations to represent our biological understanding of how social inhibition influences colony demographic transitions of workers from the nursing to foraging states, and how the colony population and food availability can influence brood rearing. To realistically model how colony populations change over time we have allowed forager bee death rates, egg laying rates and food collection parameters to vary seasonally. Even though our model is minimalistic, it manages to successfully capture many of the features of population growth in real honey bee colonies. As discussed previously, the model predicts colonies of a realistic size and with reasonable proportions of brood, nurse and forager bees (see Fig. 5b for a nominal death rate of 0.15, and Fig. 5c for close to critical death rate of 0.21).

6.2. Inferences from the model

The sensitivity analysis was an exploration of what factors in the model had the greatest influence on colony growth and development. Our objective was to determine what model parameters result in colony failure. If our model is successful as a representation of reality, these parameters should be predictive of situations in which honey bee colonies are at greatest risk. There are three classes of parameters in the model that strongly influence colony growth trajectories and the likelihood of failure. These were bee
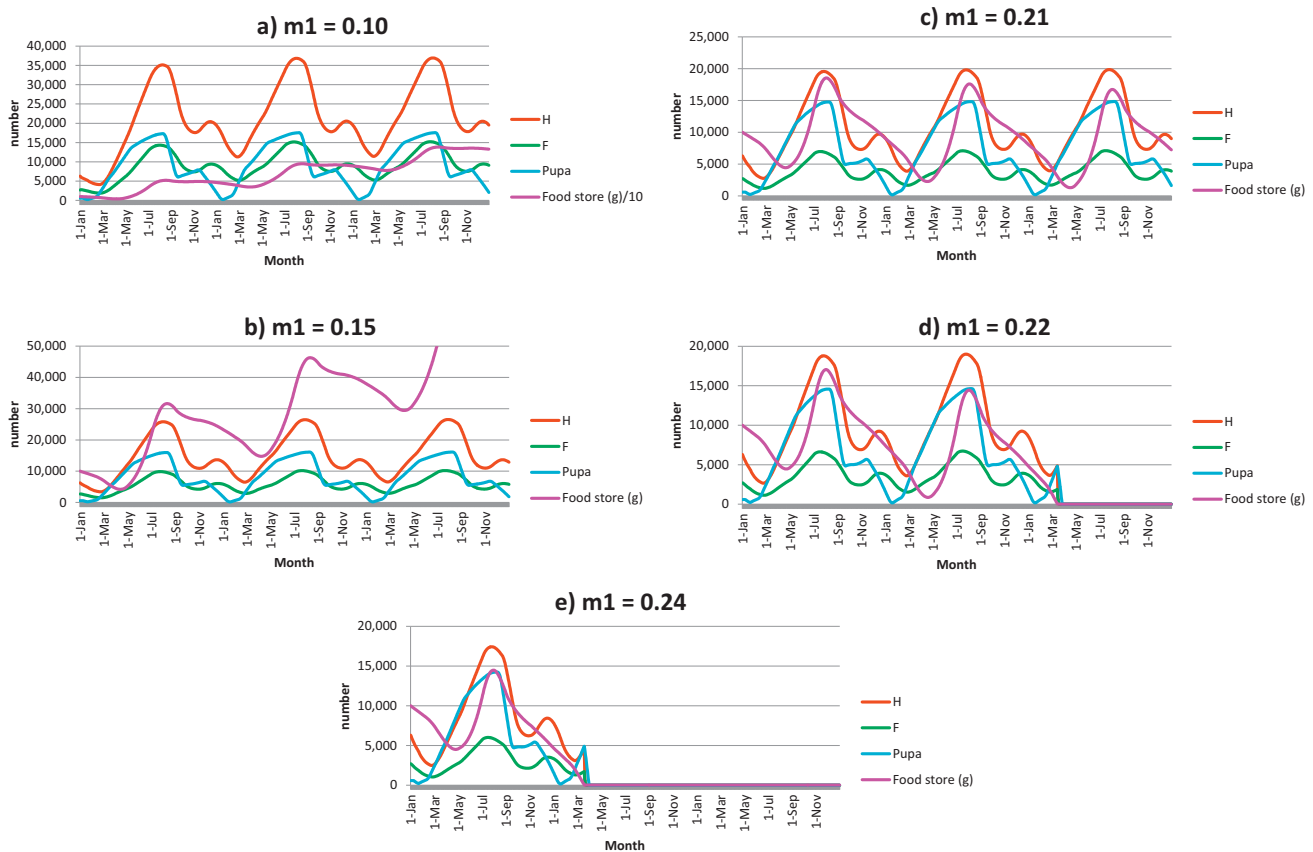
Fig. 5. Model results for the basic model simulations, with the following forager death rates, m_1 (the proportion of forager bees which die each day): (a) $m_1 = 0.10$; (b) $m_1 = 0.15$; (c) $m_1 = 0.21$; (d) $m_1 = 0.22$; (e) $m_1 = 0.24$.

mortality, factors influencing the transition of hive bees to forager bees, and factors influencing food balance (Table 4).

The critical forager mortality rate (m_1) is used as a probe to determine the sensitivity of colony failure to changes in the other parameters, and therefore it is not possible to measure the sensitivity of colony failure to changes in m_1 in the same way. However, an indication of the sensitivity of colony failure to the value of m_1 is suggested (Table 4) by noting that by changing m_1 from 0.22 to 0.24 (Figure 5(c) and (d)) in the basic model (a change of 9% in this parameter) results in a change in the day of death from Death Day 799 to Death Day 443: a change of 45% in colony longevity. The sensitivity of the day of death to the variation in m_1, therefore, would be −4.90, which is extremely strong indeed.

A strong influence of mortality rates on model outcomes is expected from population models (Schmickl and Crailsheim, 2007), and especially in this case as our base equations are derived from Khoury et al. (2011) who identified forager mortality rate as a major driver of colony failure. However, here we allowed mortality of nurse bees to vary independently from forager bees, and nurse bee mortality (m_2) did not strongly influence colony failure. Neither increasing nor decreasing m_2 significantly altered model outcomes. This is because a loss of nurse bees could be compensated by a proportion of foragers reverting to nursing roles, which effectively buffered the size of the nurse bee population.

While altering m_2 had minimal effect on model outputs, altering the rate at which nurse bees became foragers (the social inhibition parameter σ) had severe impacts on model outcomes (Table 2). Reducing σ and increasing α_{min} both effectively reduced the amount of time bees spent as nurses and increased the proportion of forager bees in the colony. Reducing σ made colonies more

resistant to failure (the critical value of m_1 increased) probably as a result of the boosted foraging force rendering the colony more resistant to starvation. Conversely, increasing σ or decreasing α_{min} effectively increased the amount of time bees spent nursing and reduced the proportional size of the colony foraging force. Both these manipulations accelerated colony death, and saw colony simulations starving to death as a consequence of compromised foraging.

Clearly, in the model σ is extremely important in determining colony fate, and it is important that it be accurately parameterised in any predictive model of a colony. A difficulty is that in real colonies σ cannot be directly measured: it can only be inferred from the proportion of hive bees and forager bees in a natural colony at equilibrium. In real colonies about 30% of bees may be acting as foragers (although not all of these will be active) (Seeley, 1985), hence we set σ at 0.75 so that our simulations reproduced the size of observed foraging forces. Our model suggests that any agent that alters σ could have an enormous impact on the development of a colony.

We know of no biological agent that could increase σ in a honey bee colony, but many factors could decrease σ. An early transition from nurse bees to foraging is caused, in part, by an elevated brain level of octopamine (Barron et al., 2002, 2007; Schulz et al., 2002a) and depleted fat reserves (Schulz et al., 1998; Toth and Robinson, 2005). This is consistent with early foraging at the individual level being a general stress response in honey bees (Even et al., 2012). It can be caused by numerous hormonal and pharmacological treatments, and even simple handling stress in early life (Ben-Shahar et al., 2002; Schulz et al., 2002b; Toth and Robinson, 2005). Individual food deprivation (Schulz et al., 1998; Toth and Robinson,

Table 4
Sensitivity analysis of colony point of death.

Parameter	Base	New	m_1 death	Sensitivity	Comments
m_2	0.007	0.020	0.18	−0.10	No starvation
b	500	2000	0.22	0.00	
σ	0.75	0.50	0.28	−0.82	No starvation
α_{min}	0.25	0.20	0.14	1.82	
α_{max}	0.25	0.20	0.22	0.00	
c_{max}	99	89	0.17	2.25	
$f(0)$ (gm)	10,000	8000	0.22	0.00	
$F(0)$	2700	1000	0.22	0.00	
$H(0)$	6300	3000	0.22	0.00	
Eggs (0)	140	0	0.22	0.00	
Larva (0)	280	0	0.22	0.00	
Pupa (0)	580	0	0.22	0.00	
γ_B (mg/day)	32.6	25	0.30	−1.56	
γ_F (mg/day)	6.7	10	0.19	−0.83	
γ_H (mg/day)	6.7	10	0.13	−0.28	
Critical food (gm)	100	500	0.22	0.00	
Critical population	1500	3000	0.22	0.00	
L_S base	0.1	0.2	0.21	0.00	
L_S – no summer dearth	0.34	0.9	0.19	−0.08	
c_S base	0.1	0.03	0.22	0.06	
c_S dearth	0.19	0.8	0.33	0.16	
Death rate seasonality base	0.29	0.2	0.22	0.00	
Death rate seasonality – no summer minimum	0.57	0.9	1.80	−0.31	
m_S – cut-in	End Feb	End Mar	0.23	0.55	
m_S – cut-out	End Nov	End Dec	0.22	0.00	
c_S cut-in	End Feb	End Jan	0.26	−2.18	
c_S cut-out	End Dec	End Jan	0.24	1.09	
L_S cut-in	End Jan	End Dec	0.23	−0.55	
L_S cut-out	End Dec	End Nov	0.24	−1.09	
Death day	30 Jun	30 Jul	0.22	0.57	

This table shows the sensitivity of the lowest m1 death rate that causes colony failure to a change in parameter, while all other parameters are held constant. The top row shows the basic model results against which the others are compared. The 'base' column shows the value of each parameter in the basic model, and the 'new' column shows the changed value of the parameter. The 'sensitivity' column gives the ratio between the percentage change in m1 and the percentage change in the parameter of interest. All colony collapses were caused by starvation, unless noted as 'no starvation' in the comments column.

2005) will also cause early foraging, as will various sub-lethal infections of adult bees, especially *Nosema* (Higes et al., 2008; Tofilski, 2002, 2009). Our model suggests that this response is effective in bolstering a colony against stressors.

Any factor that shifts the food budget of the colony into the negative (reducing the food collection factor or increasing food consumption by brood and hive bees: γ_H or γ_B) also sharply reduces colony survival. This is intuitive, and in our simulations colonies starved to death. The model outcomes were also extremely sensitive to variation in seasonal food availability and food demand. Here we modelled a situation common in some northern latitudes when laying and brood production in colonies begin to increase in midwinter in advance of the spring bloom and abundant food availability (Seeley, 1985). Elevating colony population in advance of spring primes bees to make maximum use of the spring food abundance (Seeley, 1985), but this also places colonies in an extremely vulnerable position since a colony depletes its food reserves under the expectation of being able to replenish them in spring. In our simulations most colony deaths occurred in spring, and even a small shift in colony food budget or timing of growth in this period (either delaying food collection cut in, or delaying egg laying cut in) increased colony failure (Table 4). This is important since a consequence of climate change is an increased variability in spring climate and shifts in flowering seasons (Menzel and Fabian, 1999; Walther et al., 2002; Willis et al., 2008). Our model suggests that honey bees could be especially sensitive to these changes.

A motivator for this model has been the serious concern over honey bee colony collapse disorder (CCD) (Neumann and Carreck, 2010; Oldroyd, 2007; Ratnieks and Carreck, 2010). Several features of CCD were deemed mysterious. Colonies appeared to depopulate extremely rapidly, they left both sealed brood and food reserves in the colony but no adult bee corpses were found and while many different pathogens were detected in the remaining hive boxes, there

were no obvious epidemic-levels of infection (VanEngelsdorp et al., 2009; VanEngelsdorp et al., 2010). In our model many of our simulations resulted in a small amount of sealed brood remaining at the point of colony death, but most of our simulations also ended with colonies starving to death. Colonies died leaving residual food when either nurse bee mortality (m_2) increased sufficiently, or when social inhibition (σ) decreased (Table 4). The model suggests therefore that a colony could fail displaying the features of CCD if it experiences very severe and sustained increases in both forager and nurse bee mortality, and also stress on the nurse bee population resulting in a precocious transition of nurses to foragers. A number of bee diseases could cause such a scenario, including *Nosema* and *Varroa*, both of which have been linked to some occurrences of CCD (DeGrandi-Hoffman and Curry, 2004; Higes et al., 2008; Ratnieks and Carreck, 2010). The impacts of infections on the behaviour and longevity of nurse bees, and how this may impact colony growth deserves greater attention.

6.3. Model restrictions

There are a number of ways in which our model could be improved to better simulate real colonies. The most obvious is that thus far we have treated food as combined pollen and nectar. In reality pollen and nectar are distinctly different nutrients (protein and carbohydrate respectively) that are collected by different populations of foragers. There are strong biological justifications for treating fluxes of pollen and nectar separately through colonies, and other models have adopted this approach (Schmickl and Crailsheim, 2007). However, doing this more than doubles the number of parameters that must be estimated and assumed. Harbo (1993) justified his choice to neglect the effects of pollen collection on the grounds that the energy involved in collecting the pollen balanced the energy returned from the pollen itself, and errors in

this assumption would be purely random. We chose for this first model attempt to take the simpler approach of combining pollen and nectar in our approach to food.

Our modelling of the kinetics of colony population decline is also quite basic, and very likely inaccurate. There are biological reasons to imagine that colony depopulation could accelerate once colonies become small. Small colonies will be less able to exclude or control colony pests, and properly thermoregulate their brood nests (Jones et al., 2005; Schmickl and Crailsheim, 2004). Food collection will also be compromised as a small colony will be able to survey a smaller area for available forage.

This relates to perhaps the greatest limitation of the model in that the accuracy of any predictive model would depend entirely on the accuracy of the parameterisation. Currently good data sets of how colony demography and food availability fluctuate across annual cycles (including winters) are rare, and there is almost no data for colonies outside North America and Europe. Adding factors to this model structure to consider a more accurate representation of food, or the impacts of specific diseases is quite simple, but accurately parameterising these factors will demand better empirical data.

6.4. Comparison to other modelling approaches

DeGrandi-Hoffman et al. (1989) produced the first time-based model of honey bee colony growth. This considered how seasonal variation in queen laying rate can influence colony growth and considered the transitions of bees from nursing to foraging duties to occur at fixed ages independent of environmental factors or internal dynamics. Later models considered how this structure could be affected by *Varroa* mite infection (DeGrandi-Hoffman and Curry, 2005a, Degrandi-Hoffman and Curry, 2005b). Makela et al. (1993) produced a very detailed model that considered both growth of colonies and colony reproduction via swarming. This model considered the behaviour of bees within a colony to be a dynamic rather than a fixed parameter and was influenced by the demand for foraging and nursing tasks. By far the most detailed bee population model (and the most similar to our approach) is that of Schmickl and Crailsheim (2007) who have also considered how variation in food flux can interact with colony demography. They modelled pollen and nectar flux separately and focussed on how a pollen dearth can increase pollen foraging and also lead to cannibalisation of developing brood. Both Makela et al. (1993) and Schmickl and Crailsheim's (2007) models considered a different biological understanding of the process of division of labour from the social inhibition factor we have used. They assumed that worker bees would distribute themselves between tasks (nursing or foraging) in proportion to task need. This is inspired by the Foraging-For-Work understanding of division of labour in insect colonies, which has been used as a basis for a modelling of social insect colony function (Franks and Tofts, 1994; Tofts and Franks, 1992). This approach to modelling insect division of labour has been used to explore function and organisation of ant colonies (Franks and Tofts, 1994; Svendova-Franks and Franks, 1995; Tofts and Franks, 1992), and it is definitely successful in modelling a stable division of labour (Schmickl and Crailsheim, 2007). However, there is no experimental evidence that social insect behaviour operates according to the assumptions of Foraging-For-Work models (Beshers and Fewell, 2001; Robson and Beshers, 1997). Division of labour organised by social inhibition now has overwhelming experimental support for honey bees (Beshers and Fewell, 2001; Leoncini, 2004). But every model structure is at best an approximation of reality, and it would be extremely informative to explore whether simulations derived from Schmickl and Crailsheim's (2007) approach or our model structure are more effective in simulating conditions of real colonies.

7. Conclusion

To conclude we have presented a simple modelling approach to simulate honey bee population growth through multiple years. The model is effective in simulating the performance of real colonies and indicates that disruption in food availability or social inhibition could be important causes of colony failure. This suggests that colonies may be especially sensitive to compromised forage situations, shifting seasons, or agents that reduce survival of both nurse and forager bees.

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