Multiple stressors: using the honeybee model BEEHAVE to explore how spatial and temporal forage stress affects colony resilience

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Abstract

The causes underlying the increased mortality of honeybee colonies (*Apis mellifera*) observed over the past decade remain unclear. Since so far the evidence for monocausal explanations is equivocal, involvement of multiple stressors is generally assumed. We here focus on various aspects of forage availability, which have received less attention than other stressors because it is virtually impossible to explore them empirically. We applied the colony model BEEHAVE, which links within-hive dynamics and foraging, to stylized landscape settings to explore how foraging distance, forage supply, and "forage gaps", i.e. periods in which honeybees cannot find any nectar and pollen, affect colony resilience and the mechanisms behind. We found that colony extinction was mainly driven by foraging distance, but the timing of forage gaps had strongest effects on time to extinction. Sensitivity to forage gaps of 15 days was highest in June or July even if otherwise forage availability was sufficient to survive. Forage availability affected colonies via cascading effects on queen's egg-laying rate, reduction of new-emerging brood stages developing into adult workers, pollen debt, lack of workforce for nursing, and reduced foraging activity. Forage gaps in July led to reduction in egg-laying and increased mortality of brood stages at a time when the queen's seasonal egg-laying rate is at its maximum, leading to colony failure over time. Our results demonstrate that badly timed forage gaps interacting with poor overall forage supply reduce honeybee colony resilience. Existing regulation mechanisms which in principle enable colonies to cope with varying forage supply in a given landscape and year, such as a reduction in egg-laying, have only a certain capacity. Our results are hypothetical, as they are obtained from simplified landscape settings, but they are consistent with existing empirical knowledge. They offer ample opportunities for testing the predicted effects of forage stress in controlled experiments.

Introduction

In recent years, substantial losses of managed honeybee colonies (*Apis mellifera*) in Europe and USA have been reported (e.g. Potts et al. 2010, Van Bergen et al. 2013). Currently there is increasing concern about the sustainability of managed honeybee colonies to keep up with the rising demand for insect-pollinated food production (Aizen et al. 2008). Although the underlying causes of increased colony mortality remain unclear, there is growing consensus that multiple stressors are involved (van Engelsdorp et al. 2009, Van Bergen et al. 2013, Doublet et al. 2014). The most important stressors include parasites and pathogens (e.g. Le Conte et al. 2010, Meixner et al. 2014), changes in forage quantity and quality due to land use changes (Naug 2009, Di Pasquale et al. 2013), and changing exposure to pesticides residues (e.g. Henry et al. 2012, Fischer et al. 2014).

Here we focus on various aspects of changes in forage availability. As factors relating to forage availability are virtually impossible to systematically control and vary in field experiments, we used the recently developed structurally realistic computational model BEEHAVE (Becher et al. 2014), which was designed to explore the effects of multiple stressors within a hive and in the landscape. No previous honeybee simulation model couples in-hive dynamics and pathology with foraging dynamics of bees in landscapes (Becher et al. 2013). This study is a first application of the BEEHAVE model that performed a systematically theoretical analysis to highlight when tipping points are likely to be reached with different combinations of forage stressors. In particular, we test under what conditions so-called "forage gaps", i.e. periods in which honeybees cannot find any nectar and pollen, pose a threat to a colony.

Nectar and pollen availability for honeybees vary widely in different years and regions depending on environmental conditions. Land use has changed over the recent decades leading to simplified annual cropping patterns, preponderance of monocultures, and loss and fragmentation of foraging habitats such as species-rich hay meadows and hedgerows (e.g. Kremen et al. 2002). In Europe, mass-flowering crops are dominated by oilseed rape and sunflower. These crops provide ample nectar and pollen rewards to bees for a relatively short time period which is often followed by a forage dearth in intensively farmed areas especially in June or July (Decourtye et al. 2010, Couvillon et al. 2014, Requier et al. 2015), so the phrase "the June gap" has become familiar terminology amongst beekeepers. Non-cropped areas, such as set aside, field margins and grasslands providing more continuous (although less copious) nectar and pollen resources, are scarce in intensively managed farmland (Kleijn et al. 2006). Moreover, the increase in silage production, the sowing of rye-grasses as dominant plant cover in non-cropped farmlands and hay fields, and the frequency of mowing (Plantureux et al. 2005) result in a lack of nectar and pollen (Ockinger and Smith 2007).

The honeybee is a central-place forager, and the spatio-temporal dynamics of nectar and pollen in the landscape are important to provide a sufficient energy supply (Lonsdorf et al. 2009), so foraging distances between hive and flowers matter. They depend on the seasonal abundance of profitable forage resources and range from a few hundred metres in forage-rich agricultural landscapes (Free 1993, Steffan-Dewenter and Kuhn 2003) up to several kilometres in a patchy landscape (Visscher and Seeley 1982, Beekman and Ratnieks 2000). Previous field studies report that the foraging radius of honeybee colonies expands if the availability of nectar and pollen is temporarily low (Steffan-Dewenter and Kuhn 2003). Larger foraging distances, though, imply less energetic efficiency of foraging and increased forager mortality, which can affect both colony size and survival.

In this study we used the honeybee model BEEHAVE (Becher et al. 2014) to simulate how forage gaps affect colony resilience and dynamics. We model the combination of timing and duration of forage gaps with two other factors: foraging distance and overall forage supply. To be able to control these factors in a systematic way, we are using a highly stylized landscape consisting of a single forage patch. Exploring more realistic landscapes requires compiling data on farming practice, and nectar and pollen supply of crop and non-crop plants, which will be presented in a follow-up study.

In the present study, we explored the following hypotheses: (1) forage availability and foraging efficiency, which are determined by overall supply of nectar and pollen and foraging distance, strongly affect colony dynamics and resilience of a simulated honeybee colony; (2) temporary gaps in nectar and pollen supply ("forage gaps") affect colony dynamics and resilience. The ability of a honeybee colony to cope with forage gaps depends on timing and duration of the gaps; (3) the different attributes of forage availability, which may act as stressors, interact, i.e. a combination of these stressors that are individually at sub-critical levels may still put a honeybee colony at severe risk.

Methods

The model BEEHAVE

BEEHAVE is a computational honeybee model that integrates in-hive colony dynamics, in-hive mite population dynamics, mite-mediated disease transmission, and foraging for nectar and pollen in heterogeneous and dynamic landscapes (Becher et al. 2014). Its purpose is to explore how various stressors, and their interactions, affect the structure and dynamics of a single honeybee colony. BEEHAVE includes many submodels and parameter values from earlier models that focussed on single compartments and stressors (Becher et al. 2013).

The colony model is cohort-based and describes, on a daily basis, in-hive colony structure and dynamics driven by the queen's egg-laying rate. Mortality rates depend on the bees' developmental stage, disease status and colony conditions such as ratio of brood to nursing bees and honey and pollen stores. The mite model describes the dynamics of a varroa mite population within the honeybee colony and the transmission of e.g. deformed wing virus. The foraging model, executed once per day, represents the bees' foraging behaviour with weather conditions affecting the daily time allowance for nectar and pollen collection. Landscape features, including changes in availability of nectar and pollen, can be updated every day.

BEEHAVE is implemented in the freely available software platform NetLogo (Wilensky 1999). BEEHAVE, its extensive documentation following the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, 2010), and a user manual are freely available (www.beehave-model.net). The parameters and model assumptions and equations which are most relevant for understanding the scenarios explored in this study in detail are listed in Tables A1 and A2 in the supplementary material.

Initial settings

We used most of the BEEHAVE default settings, starting all simulations on 1st January with an initial colony size of 10,000 worker bees, no infestation with virus-infected varroa mites and no beekeeping practices were included (Becher et al. 2014, Appendix S5). Varroa mites were not included, as untreated colonies die within a few years due to varroa-transmitted viruses (Becher et al. 2014). This would have strongly limited the insights we gain from the simulations on the impact of forager availability. Colonies efficiently treated against varroa in contrast do not differ in the model from colonies without varroa mites (Becher et al. 2014).

To be able to vary stressors in a systematic way, we chose a highly stylized landscape and constant average weather conditions. The landscape consisted of a single forage patch providing constant amounts of nectar and pollen throughout the foraging season except for forage gaps (see below). Weather defines the daily foraging period and was assumed to constantly allow for a daily foraging period of 8 hours within the foraging season (see Appendix Tab. A1). A daily foraging period of 8 hours seems to be sufficient to not restrict colony growth (e.g. Schmid-Hempel and Wolf 1988, Seeley et al. 1991) and ensures that detected effects of forage stress on colony dynamics are not obscured by the effects of varying weather conditions.

In pre-runs of the model we found that a foraging season from day 80 to day 290 (March 21 and October 17) and a sugar concentration of 1.5 mol / l (51 %) allowed for long-term colony persistence (see Appendix Figs. A1, A2, A3).

Stressors

To tease apart the influence of different aspects of forage availability, we defined stressor settings relating to forage distance, supply and forage gap (Table 1). We did not modify within-hive processes. In particular no mite infestation or diseases were simulated, and we did not include pesticide-induced forager mortality.

Foraging distance

The flight distance from the hive to the forage patch affects foraging costs in terms of time, energy expenditure and forager mortality. The mean observed foraging radius of honeybees' ranges from several hundred metres (Free 1993), and 1526 m (Steffan-Dewenter and Kuhn 2003), up to 5500 m (Beekman and Ratnieks 2000) depending on spatial and temporal context. Pre-runs indicated that foraging distances exceeding 2000 m led to colony failure within the third year at latest (see Appendix Fig. A2 and A4). Thus, we focused on foraging distances of 500, 1000 and 1500 metres from the hive to the single forage patch.

Forage supply

Regarding high variability in overall nectar and pollen supply in agricultural landscapes, we simulated two extreme forage supplies, high and low. High forage supply was defined as 100 l nectar and 100 kg pollen per day representing a forage surplus, because nectar and pollen production over blooming period of mass-flowering crops such as oilseed rape was estimated up to 170 kg pollen and 200 kg nectar per hectare (Illies 2010). With this supply, colony growth is not limited by the amount of food offered in the patch. In contrast, under a low forage supply of 3 l nectar and 0.5 kg pollen per day according to Becher et al. (2014), colonies were, for the foraging distance of 1000 m, already at the brink of starvation. For both levels of forage supply, the respective amount of nectar and pollen at the single patch was replenished every day.

Under low forage conditions, the available nectar and pollen amounts at the forage patch can be completely depleted on a given day. Consequently, according to the model assumptions regarding foraging (see Appendix Tab. A2), handling time, i.e. the time a forager needs to collect a nectar or pollen load at the patch, increases with the degree of forage depletion at this patch. Handling time in turn strongly influences the duration of a foraging trip. Thus, under low forage supply, energy expenditure and foraging mortality per trip tend to be higher.

Timing and duration of forage gaps

We simulated temporary lack in nectar and pollen supply by defining forage gaps in which the daily availability of nectar and pollen was set to zero, but constant weather conditions still allow searching trips within this time. Forage gaps always started on the first day of a given month within the foraging season, lasting for 3 up to 30 days and were explored for each month between April and September separately. The exact timing and duration of a forage gap of a given scenario were repeated in each of the five simulation years.

In pre-runs of combinations of timing and duration of forage gaps, short-term (6 days), middle-term (15 days), and long-term (21 and 30 days) forage gaps showed very different effects on honeybee colony size on December 31(see Appendix Fig. A4). During induced forage gaps, larvae and adult bees use stores of pollen and honey. If these stores become low, foraging probability and also foraging trips per hour increase.

Experimental design and analysis

To investigate colony resilience we systematically explored risk of colony extinction for all combinations of our forage stressors: foraging distance, forage supply, and timing and duration of forage gap (Table 1). To understand the mechanisms behind these extinction results, we also explored the effects of these stressors on actual colony dynamics for a selected set of scenarios (Table 2). This is feasible because the BEEHAVE model incorporates detailed processes of energy income and storage in the hive, development of different life stages, task allocation amongst workers and feedback loops reflecting the biology of a colony (Becher et al. 2014). We ran simulations for all scenarios for five years to capture how effects of forage stress, that has subcritical effects on a honeybee colony in the first year, can build up over several years and cause colony failure and for 30 replicates to capture extinction risk and variability in output due to stochastic processes.

Colony extinction analysis

We quantified risk of colony extinction as the percentage of colony losses within five simulation years. A colony was considered extinct if the number of adult bees fell below 4000 bees on December 31 or went down to zero within the season (Becher et al. 2014).

For all colonies that were lost within five years, we calculated the average time (number of days) to colony extinction, and the percentage of lost colonies which died due to winter mortality or due to starvation within a season. When the colony size on December 31 fell below the critical threshold (4000), winter mortality caused colony extinction. Colony extinction due to starvation occurred if honey stores were completely exhausted, resulting in the immediate death of all brood and adult bee stages.

To evaluate how much variation in colony extinction, causes of colony extinction, and time to colony extinction can be explained by our four forage stressors, we performed variation partitioning. All statistical analyses were conducted using R version 3.1.2 (R Development Core Team 2014). We used the modEvA-package (Barbosa et al. 2015), specifically the varPart function, which allows partitioning of the variation up to three explanatory factors (e.g. Real et al. 2003).

Firstly, we defined colony extinction and colony extinction due to starvation as binary data (0 = colony survival; 1 = colony death within five simulation years). For these response variables we fitted two separated generalized linear models (GLZ) with binomial error distribution and logit link (i.e. logistic regression) that included all four explanatory factors and all their two-way interactions. Similarly, for the response variable time to colony extinction (prior log-transformed, to achieve normality), we fitted a GLZ with normal distribution and identity link including all four explanatory factors and all their two-way interactions. To find the best model and to retain not more than three explanatory factors (as more is not supported by varPart function), we conducted model selection with AIC on the above-described GLZs using the MuMIN package (Bartoń 2014), and we dropped the stressor forage supply as it occurred rarest in the subset of the best models as identified with AIC. Prior to variation partitioning we conducted residual analyses of the fitted models by checking the normality of residuals and plotting them versus each explanatory variable. Normality was satisfied and no conspicuous patterns in residuals were detected, therefore models were judged as satisfactory.

As the best model includes most of the parameters, we conducted variation partitioning for each of the response variables using the three explanatory factors foraging distance, timing of forage gap and duration of forage gap and their two-way interactions as the full model. For this, we calculated Spearman rank correlation coefficients between the model predictions obtained with each single factor (and their combinations) and the predictions from the full model (e.g. Muñoz and Real 2006). These correlation coefficients were then used to estimate the proportional contribution of each factor and each factor combination to the total variation explained by the model.

Colony dynamics: Exploring effects of single and combined forage stressors

Scenarios which showed contrasting impacts on colony extinction (Tab. 2, Fig. 1) were selected to explore effects of forage stressors (alone or in combination) on colony dynamics.

Forage distance: We examined how increasing foraging distance from 500 m (nearby foraging) to 1500 m (distant foraging), under continuous high nectar and pollen supply, affects colony dynamics (no forage gap).

Forage supply: We explored the impact of high forage supply versus low forage supply, fixed at an intermediate distance of 1000 metres from the colony (no forage gap).

Combining forage distance and supply: To analyse the interaction, we combined all possible combinations of these two factors.

Forage gap: To understand how different timings of forage gaps influence the processes shaping colony dynamics, we simulated a middle-term forage gap of 15 days and an intermediate distance of 1000 m, because at this distance forage availability was good enough for colonies to survive under both high and low forage supply. Moreover, we assumed that a forage gap of 15 days may frequently occur in agricultural landscapes. To identify the characteristic indicators and mechanisms accompanying colonies thriving or failing in response to timing of a forage gap, we distinguished three patterns of colony development. We selected timings of forage gaps, where i) colonies died quickly due to starvation, ii) colonies declined continuously until they die during winter and iii) surviving colonies, which coped well with this temporal forage gap.

To analyse how forage stressors affect colony dynamics, we retrieved output from the BEEHAVE simulations on the quantity and cause of mortality of brood and adult stages. We focused on effects of forage stressors on queen's egg-laying rate (quantified by the number of eggs by which the potential egg-laying rate was reduced, referred to as 'eggs: not laid') and the mortalities of eggs and larval stages caused by insufficient number of available nurse bees and the lack of pollen. For example ‘larvae: pollen’ indicates the number of larvae that died in a model time-step (a day) due to lack of protein from pollen (Table 3).

To compare selected scenarios, we calculated the differences in mortalities between the stress scenarios explored and the most favourable forage scenarios (the latter indicated in the plots as zero lines). For combinations of forage supply and foraging distance, the most favourable forage scenario was defined as high forage supply and 500 m foraging distance. For comparison of selected forage gap scenarios, we used high forage supply, a foraging distance of 1000 metres, and no forage gap as most favourable forage scenario. To understand if the honeybee colony is able to satisfy its forage demand to survive over winter under forage stress, we analysed monthly averages of colony size, honey stocks, foraging trips per hour, and percentage of forager losses caused by different processes (mortality risk of foraging, exceeding their maximum flight distance, or maximum lifespan).

Results

Colony extinction

Risk of colony extinction after five years varied with foraging distance, timing of induced forage gap, forage gap duration in the respective month, and overall forage supply (Fig. 1). In our hypothetical landscape, where one single patch provided continuous amounts of nectar and pollen, for a foraging distance of 500 m, few colonies were lost, unless under prolonged forage gaps. Foraging distances of 1500 m always resulted in very high colony losses independent of forage supply and timing and duration of forage gaps. For a foraging distance of 1000 m, the timing of the forage gap was important, where gaps in June and July had the most severe impact. While a 15 day forage gap induced in June or July led to colony extinction in most cases (≥ 80 %) under both forage supplies, such a forage gap induced in e.g. May or September did not cause colony failure under high forage supply. Reduced amount of food offered at the patch worsened the situation of the colonies. Forage gaps that lasted 30 days caused about 80 % colony losses independent of their timing and forage supply.

Increasing flight distance to the forage patch led to earlier colony extinction and increased the probability of starvation. Low forage supply caused earlier colony extinction than high forage supply, but the percentage of colony losses driven by starvation was largely independent of the level of forage supply. For forage gaps induced in June and July, colonies died the quickest (within one or three years) and mainly due to starvation. When forage gaps were induced in April, May or September, colonies mainly died due to winter mortality and this happened after two to five years, indicating that colony size continuously declined. Increasing duration of forage gaps led to earlier colony extinction in general (Fig. 2).

Most variation in colony extinction was explained by foraging distance (0.288), followed by duration of a forage gap (0.158), and by timing of a forage gap (0.092). Moreover, 0.287 of variation was explained by common contribution of these factors (Fig. 3A). Colony extinction due to starvation and time to colony extinction were affected to a large degree by timing of the forage gap (0.782 and 0.557), followed by duration of a forage gap (0.166) for time to colony extinction (Fig. 3 B, C).

Colony dynamics

Foraging distance

If colonies only had access to a distant forage patch, then yearly peak and overwintering colony size was reduced (Fig. 4 A). Already in the first year distant foraging caused an additional peak of reduced egg-laying in June and much higher mortalities of eggs and larvae in June and July due to an insufficient number of available nurse bees compared to nearby foraging (Fig. 4 B, C). On average, distant foraging resulted in lower foraging trips per hour in August and September, distinctly reduced honey stores, and caused higher forager losses in September (Tab. 4), where colony size and thus workforce is low anyway.

Forage supply

Low forage supply led to declining colony sizes from the second year on, and overwintering colony size was substantially lower in the fifth year compared to high forage supply (Fig. 5 A). In the fifth year, the peaks of eggs not laid and eggs and larvae lost due to insufficient number of nurse bees in

June and July were much higher under low forage supply (Fig. 5 B, C). On average, low forage supply caused fewer foraging trips per hour, lower amounts of stored honey and higher forager losses in September of the fifth year (Tab. 4).

Combining foraging distance and forage supply

On average, more accessible food (high forage supply at 500 m) led to higher colony size, honey stores and more foraging trips per hour, especially in August and September, than all other combinations (Fig. 6 A, C, E). These effects were already visible in the first year, but much more pronounced in the fifth year of simulation (Fig. 6 B, D, F). Compared to high forage supply at 500 m, the daily number of eggs not laid and number of eggs and larvae died due to insufficient number of available nurse bees in June and July, distinctly increased with foraging distance of 1000 m under low forage supply and independent of food supply for a foraging distance of 1500 m (Fig. 7 A, C, E). These effects were more pronounced in the fifth year (Fig. 7 B, D, F).

Forage gap

For an intermediate foraging distance of 1000 m under high forage supply, the timing of a 15 day forage gap determined the fate of a colony (Fig. 8A). When the gap occurred in May colonies still showed a viable colony development pattern with a peak size of ca. 25000 bees (Fig. 8 A). Their honey stores were increasing during summer culminating in more than 30 kg by the end of September (Fig. 8 B, C). This allowed the colony to reduce their foraging efforts in September, so lower number of foraging trips and modest forager losses in September similar to most favourable forage scenario (high forage, no gap) ensured colony sizes large enough to survive the winter (Fig. 8, D, E, Tab. 4). A May gap showed a higher daily number of eggs not laid in June and July of the second years compared to no gap situation (Fig. 9 A, B), but no losses of larval stages due to a lack of protein (Fig. 9 C, D).

A 15 day forage gap in June or July disturbed the colony development severely even in the first year, so peak colony sizes of only 20000 bees or less and colony's honey stores in September below 22 kg were distinctly lower compared to May gap (Fig. 8 A, B, C, Tab. 4). The number of foraging trips in August was lowered and forager losses in September were higher compared to the

May gap (Fig. 8 D, E, Tab. 4). Reduced egg-laying rate and large losses of larvae during the gap (Fig. 9 A, C) at a time when the queen's potential egg-laying rate is near its maximum reduced colony size (Fig. 8 A), and thus the workforce of nurse bees and foragers. Consequently, the colonies had to keep their foraging activity relatively high in September to avoid starvation during winter, resulting in further losses of foragers and weak colonies in spring (Fig. 8 A, E, Tab. 4). Small colony sizes then limited the egg-laying rate of the queen (Fig. 9 B), again. Hence, colony growth in the second year was already diminished even before another forage gap with further loss of larvae occurred (Fig. 9 D). This lead to a gradual decline of the colony over several years until it finally failed. For gaps in June or July, no colonies were left alive after four or five years.

If the colony was already challenged by reduced forage availability, then a 15 day forage gap in July ('July Gap, low forage') had devastating effects on colony size and honey stores (Fig. 8 A, B, C). Foraging trips were lowest in August and September (Fig. 8 D, E, F). Such a July gap under low forage supply caused strongest reduced egg-laying rate of the queen and largest losses of larvae due to protein lack (Fig. 9 A-D). Thus, colony size and workforce was distinctly reduced. Reduced foraging efforts and highest forager losses in September (Tab. 4) induced a high probability of starving to death during the forage gap, as the low honey stores were not sufficient to bridge it. Eight colonies died during the July gap in the first year, all other colonies died within the second year latest.

Discussion

A range of stressors have been discussed as having responsibility for the observed honeybee colony losses and decline of colony health. Parasites, pathogens and pesticides have been widely suggested as major drivers (Le Conte et al. 2010, Henry et al. 2012, Fischer et al. 2014, Meixner et al. 2014, Doublet et al. 2014), but the influence of forage availability in the landscape has received less attention because of the difficulty of conducting empirical studies.

Forage availability is also a multi-dimensional factor. It is not just a matter of how much there is in a landscape, but it matters where the flowers are and when they occur, and over what time period. We therefore focused in this study on these aspects, and in particular on the short- and long-term consequences of forage gaps. Such gaps may be induced by bad weather, large-scale intensively managed monocultures of crops, or both.

We hypothesized that the resilience and extinction risk of a honeybee colony will depend on various parameters relating to forage availability (stressors) alone and in combination. We investigated how honeybee colonies cope with different levels of the forage stressors: overall forage supply, the foraging distance to forage source, and the timing and duration of temporal forage gaps. The latter was assumed because there are likely to be times in a year where typical colony development depends on continuous input of forage, in particular pollen which cannot be stored for very long.

We used the model BEEHAVE to create scenarios representing different combinations of these stressors, because no previous honeybee simulation model couples in-hive dynamics and pathology with foraging dynamics of bees in landscapes (Becher et al. 2013).

Our results demonstrate and quantify, for the first time, that indeed forage gaps of about two weeks, which may frequently occur in reality, can lead to colony losses if the colony is already stressed and struggling to survive due to limited forage input caused by longer foraging distances or overall low availability of nectar and pollen, or if the gap occurs in months where the colony is particularly sensitive. So, for a forage distance of 1000 m, which is still close enough for colonies to survive, sensitivity to forage gaps of 15 days was highest in June or July even under high forage supply. Poor forage supply accelerated extinction and increased probability of starvation, but had a lower influence than the other factors (Fig. 1, 2, 3). In the following we will discuss the main model mechanisms underlying the effects of the forage stressors alone and in combination and whether the identified mechanisms simulated in BEEHAVE, are realistic and transferable to real colonies.

Foraging distance

Increasing foraging distance even under high forage supply resulted in colony extinction after four years. Due to longer flight distances for nectar and pollen intake, foraging costs in terms of energy expenditure were higher. To be able to still satisfy the nutritional demand of the colony, colonies increased their forager workforce (data not shown). This led to a lowered number of available nurse bees. Workforce of nurse bees is linked, via model mechanisms (see Appendix Tab. A1), to the queen's egg-laying rate and to brood mortality. Thus, in June of the first year the queen's egg-laying rate was reduced resulting in fewer eggs being laid. Furthermore, high losses of eggs and larval stages occurred in June and July (Fig. 4 B, C).

Considering that from mid-June to mid-July the queen's potential egg-laying rate is at its maximum and the number of newly emerging immature and adult worker stages is highest, these losses of brood stages resulted in reduced peak colony size, and thus in overall weakened workforce, also for foraging. Honey stocks and colony size declined over the second and third year. In the fourth year, several colonies were no longer able to compensate for high losses of brood stages and foragers and were thus driven to extinction.

Forage supply

A constant low forage supply, at a flight distance of 1000 m, did not result in colony extinction within five years as long as the colony was not confronted with an additional stressor. Still, poor forage supply over the whole foraging season resulted in reduced foraging activity in August, reduced honey stocks, and higher forager losses in September. Similarly to scenarios with large foraging distances, the queen's egg-laying rate was reduced and also larvae were lost due to an insufficient nurse bee workforce. But in contrast, under poor forage conditions, the increase in brood stage mortalities and the reduced workforce for nursing and foraging tasks imposed a gradual but continual drain on the colony, building up over time (Fig. 5 A - C).

Combining foraging distance and forage supply

Adding another stressor (increasing foraging distance) caused greater sensitivity to stress imposed by low forage supply and reduced the colony's resilience (Fig. 6 A - D). Again, reduced egg-laying and increased mortality of eggs and larvae were the main mechanisms by which the colony was affected (Fig. 7 A - F). The reduction in queen's egg-laying is actually beneficial to the colony as it avoids loss of brood stages and hence wasting of resources, but poor forage over time led to reduced egg-laying in every year. This weakened colony size, and thus workforce for nursing and foraging.

These findings are likely to be robust: colonies with forage resources only available remotely will not only suffer limited nutritional intake due to longer flight distances, but their foragers will also incur higher forager mortality than colonies with forage resources more accessible. Certainly, the single-patch landscape used is simplified, and further scenarios representing realistic spatial structure and temporal dynamics of floral resources will be needed. Real honeybee colonies may be able to compensate for much greater foraging distances, but the greater the distance between the hive and a crop the greater the amount of energy consumed and the lower the honey stocks (e.g. Free and Williams 1974).

Field studies suggested that honeybees are able to gain an energy surplus at long-range foraging distances, if distant forage resources are profitable, due to their recruitment system (Visscher and Seely 1982, Beekman and Ratnieks 2000). In reality honeybee colonies shift between seasonal short- and long-range foraging depending on floral abundance in the environment (Couvillon et al. 2014) to exploit profitable resources. This may buffer colonies from building-up weakening effects.

Forage gaps

Cropping patterns in intensively managed farmland lead to monocultures of mass-flowering crops at large spatial scales that provide ample nectar and pollen rewards to honeybees for a relatively short time period followed by a forage dearth (Decourtye et al. 2010, Requier et al. 2015). In our simulations, we concentrated on a forage gap of 15 days, repeated this gap every year at exactly the same time, and set foraging distance to 1000 meters.

In BEEHAVE the queen’s potential egg-laying rate is at its maximum from mid-June to mid-July and the number of newly emerging brood stages developing into adult worker bees is highest. To achieve peak colony size and to ensure sufficient honey stocks to survive winter, it is necessary that the colony can satisfy its demand for nurse bees which take care of all brood stages and to ensure sufficient pollen stores to maintain the protein content of the jelly fed by nurse bees.

If pollen stores are depleted, larval stages die due to lack in protein content of jelly. Honeybees store much less pollen than nectar, so in our model after six days without pollen intake, pollen stores have been depleted. This is in accordance with observations of real honeybee colonies (Blaschon et al. 1999).

A May gap showed subcritical effects on colony dynamics because in this month the queen's egg-laying rate is still below its maximum. Consequently, cascading effects of reduced egg-laying and increased brood mortality were modest. Foraging activity in late summer from June to September was similar to the most favourable situation and ensured sufficient honey stores to survive winter, the colonies were thus "thriving".

In contrast, a July gap under low forage supply had detrimental effects on colony dynamics. During the forage gap and as long as the colony's pollen stores were sufficient, foraging activity was lowest and most foragers remained inside the hive. After six days of this forage gap in July, the pollen stores were completely exploited. In response, the colony increased the ratio of foragers to in-hive bees and foraging activity increased until the forage gap was over and exploited pollen stores could be filled up again. At the same time, though, high larval mortality due to pollen lack caused by the forage gap led to strongly reduced force of worker bees for nursing and foraging tasks in the colony. In turn, fewer foraging trips were performed during August and September, and much less honey was stored to survive the first winter. In the following year the small colony was not able to maintain a sufficient workforce of nurse bees and foragers. The cascade of high larval mortality, weakness in workforce and depletion of colony's stores drove colonies to extinction due to starvation within the second year.

A forage gap in June or July under high forage supply had effects that were between those of "thriving" and "starvation" colonies; colony size and colony's stores declined over time and colonies were driven to extinction within four or five years. The mechanisms responsible for this were the same as before: reduced egg-laying, increased larval mortality, and reduced workforce for nursing and foraging.

Patterns observed in reality

We have demonstrated that we can fully explain the observed effects of forage gaps and the other stressors by the interacting and cascading effects of model mechanisms that describe the effect of reduced forage input on the queen's egg-laying rate, larvae and workers. In a few cases empirical evidence exists that the same mechanisms might be relevant in reality that, so outcomes of this study using the honeybee simulation model BEEHAVE reflected some patterns observed in reality. But in general the mechanisms discussed above should be considered as hypotheses which can be tested in experiments. Such tests would either confirm the realism of BEEHAVE, or lead to more realistic versions of the model mechanisms.

Field studies suggest that during times of poor forage and as long as the colony's pollen stores are sufficient, foragers remain inside the hive to conserve their flight energy (Visscher and Seeley 1982). Because honeybees store only a small amount of pollen, stores quickly diminish during forage dearth periods (Schmickl and Crailsheim 2002). Brodschneider and Crailsheim (2010) discussed that larvae are especially dependent on sufficient pollen stores and negative effects of pollen shortages causing reduced brood production may weaken colonies. During periods of pollen shortage honeybees cannibalize young larvae to maintain older larvae (Schmickl and Crailsheim 2002).

Forage availability in real landscapes

In realistic landscapes occurrence of forage resources strongly differs between different regions. Changes in land-use and agricultural practices have resulted in loss and degradation of foraging habitats. Consequently, in many regions the availability of forage resources has become critically limited (e.g. Carvell et al. 2006). In Europe, monocultures of mass-flowering crops at large spatial scales provide ample nectar and pollen rewards to honeybees for a relatively short time period followed by a forage dearth (Decourtye et al. 2010, Requier et al. 2015).

However, forage availability to bees may vary widely among locations and land-use types, for example urban areas may provide high-quality continuous forage throughout the season to support insect pollinators (Baldock et al. 2015).

Still, in many real landscapes honeybees may be buffered from such temporal gaps in forage availability, if these occur at a small local scale (Carvell et al. 2006) due to their foraging distances exceeding several kilometers (Visscher and Seeley 1982, Beekman and Ratnieks 2000). In several field studies it was found that summer (in particular June and July) is a more challenging foraging season than spring, and honeybee foraging distances are much greater (Couvillon et al. 2014, Garbuzov et al. 2015) – hence the phrase "the June gap" has become familiar terminology amongst beekeepers. Naug (2009) suggests that nutritional stress caused by deficiencies of monocultures in forage quantity and quality may be responsible for high colony losses. Bumblebees and solitary bees in contrast to honeybees rely on individual exploration to find resources in the landscape and store much less or no nectar and pollen. Thus, land-use changes resulting in temporal forage gaps are likely to cause more detrimental effects to them, especially for such bee species with restricted foraging ranges. Insufficient diverse diets in landscapes are likely to reduce their health and stress resilience (Vaudo et al. 2015) to a much greater extent.

Beekeepers feed sugar solutions and pollen supplements, and move honeybee hives to locations with temporary rich forage resources. Still, recent reviews point out that starvation due to long non-foraging periods, and insufficient and untimely feeding, is a common reason for honeybee winter mortality (Brodschneider et al. 2010). So it is important to show what can happen if honeybee colonies are not supported with forage supplements during most vulnerable times to temporal lacks in forage availability.

Limitations

BEEHAVE allows us to implement forage availability of real landscapes. Importing information about landscape structure and crop types and timing via GIS input would be relatively straightforward. However, information about the amount and dynamics of nectar and pollen produced by the different crop and vegetation types is not readily available and requires many simplifying assumptions. Still, even with this information it would be impossible to systematically explore the effects of the three aspects of foraging because each real landscape provides just one specific configuration.

We therefore chose to use a highly stylized landscape, consisting of only one forage patch. This patch represents the average flight distance in a given landscape, and we made the simplifying assumption that this average distance remains constant within and between years. Furthermore, we assumed that forage availability is either constantly high or low, i.e. nectar and pollen are replenished to their given values at the end of each day. We also assumed constant weather conditions, with eight hours per day of suitable conditions for foraging.

Moreover, we did not consider diseases and their management options that also affect honeybee health. But parasites and pathogens can intensify the effect of forage stress (e.g. Naug and Gibbs 2009). Our assumptions about weather, forage availability, and uniform flight distances ignore so much temporal and spatial variability in real landscapes that it remains an open question, to what extend forage gaps will lead to extinctions in real landscapes. A further simplification in our model is that we assumed the gaps to occur at the same time every year. All these assumptions were needed to understand how, as a single stressor, forage gaps might affect a colony. Only based on such understanding we would benefit from exploring the effects of real landscapes on honeybee forage and, in turn, colony health, which we will do in follow-up studies.

Nonetheless, the main findings of these simulation runs are likely to be robust: honeybee colonies will be more vulnerable to forage gaps at certain times of the year but such short-term dearth alone would be unlikely to lead to colony extinction.

Multiple and other stressors

Low forage supply or extensive foraging distance made colonies more vulnerable to forage gaps. The mechanisms leading to this were in all cases similar and thus consistent. Simulations showed that effects of induced forage gaps depend on their timing and duration. The latter is in accordance with suggestions that a stressor must have chronic impact before effects are noticeable (Bryden et al. 2013), so forage dearth periods of a few days did not result in visible effects, as pollen stores were large enough to bridge these short gaps. Thus, multifactorial stress in terms of overall poor forage availability (forage supply and distance), and temporal forage gaps is likely to notably reduce honeybee resilience and to cause colony failure. Moreover, in accordance to Becher et al. (2014) the timing and the magnitude of a stressor may be important and weakening effects of one stressor may be enhanced by other stressors.

The effect of other stressors, which we did not include, is likely to affect colony structure and health via other mechanisms. Exploring their effect, in isolation and in combination with foraging stress, will thus require separate in-depth analysis of BEEHAVE scenarios.

However, in contrast to other pollinators such as bumble bees and solitary bees, the structure of a honeybee colony provides a certain buffering capacity against reduction in workforce due stress-induced mortalities (EASAC 2015). In general, bee populations are assumed to be threatened by combined stressors of parasites, pesticides and lack of forage (Goulson et al. 2015).

Conclusions

Awareness of the importance of multiple stressors is increasing, but evidence of interacting effects is scant (Potts et al. 2010, Vanbergen et al. 2013). Thus, we believe that our systematic analysis of forage stressors in a hypothetical environment improves our knowledge of how forage stressors alone or in combination affect honeybee colony resilience. Our main findings are likely to be robust: the effects of forage gaps depend on their timing and duration, and whether the colony is already under stress. The BEEHAVE model captures the complexity of the honeybee colony cycle and feedback loops such that the effect of forage stress on each life stage and on the colony's overall food or pollen debt could be examined. Forage stress affected colony dynamics in terms of reduction in new-emerging brood stages developing into adult workers - particularly through reduced egg-laying, pollen debt and lack of nursing - and also changed levels of foraging activity. It also demonstrates that feedback loops, such as a reduction in egg-laying rate, can allow a colony to adjust its development in tune with the forage provision by the surrounding landscape, but this buffer mechanism has only a certain capacity, which depends on all aspects of forage availability.

Our results are hypothetical, but consistent with existing knowledge and they offer ample opportunities for testing the identified mechanisms and predictions via controlled field or semi-field experiments. Moreover, our results can inform land management strategies and policies aimed at boosting forage provision for pollinators in agricultural landscapes.

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Tables Legends

Table 1: Settings of forage stressors.

Stressor	Parameter (referred as)	Unit	Setting
Foraging distance	DISTANCE_G (distance)	m	500, 1000, 1500 or 2000
Forage supply	QUANTITY_G_l (Nectar)	l	100 or 3
	POLLEN_G_kg (Pollen)	kg	100 or 0.5
Forage gap	Timing	- (starting from the 1st of the respective month)	April, May, June, July, August or September
	Duration	days	6, 15, 21 or 30

Table 2: Selected scenarios and their corresponding parameter settings.

Scenario	Distance (m)	Nectar (l)	Pollen (kg)	Timing	Duration (days)
				of forage gap	
Nearby foraging	500	100	100	-	-
Distant foraging	1500	100	100	-	-
High forage supply	1000	100	100	-	-
Low forage supply	1000	3	0.5	-	-
July gap, high forage	1000	100	100	July	15
June gap, high forage	1000	100	100	June	15
May gap, high forage	1000	100	100	May	15
July gap, low forage	1000	3	0.5	July	15

Table 3: Mortality variables used to example the effects of colony dynamics

Each mortality variable is named in two parts - “the life stage that is affected: the process causing that effect”. ‘Today’ is used in the explanation because these variables are calculated during the model run at the end of each simulated day.

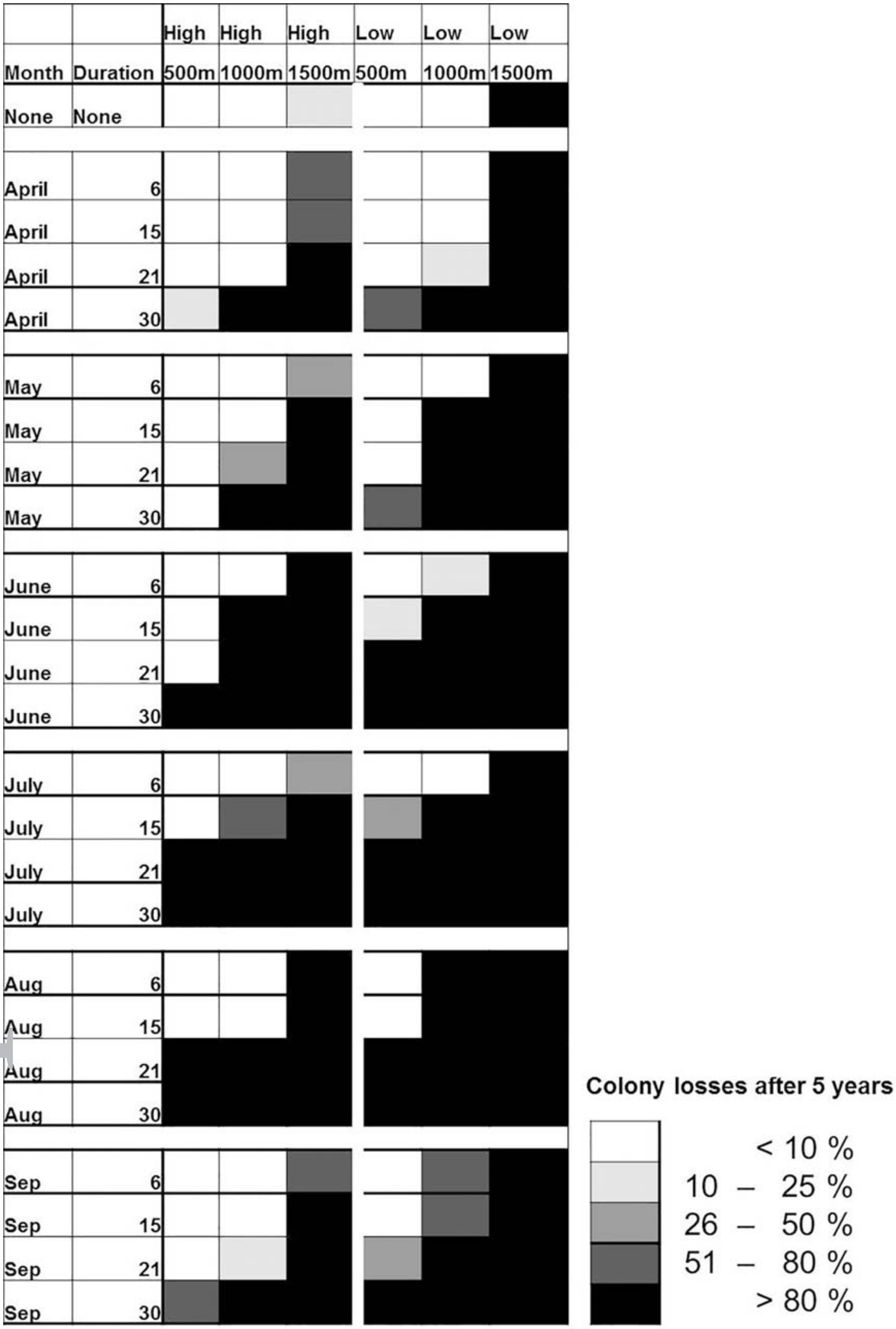
Mortality variable	Explanation
Eggs: not laid	difference between potential (season-dependent, with max. 1600 eggs per day) and actual number of eggs laid (depending on number of available nurse bees) today as a consequence of a lack of nurse bees. This reduces the future and more expensive loss of brood. The daily egg laying rate of the queen can be reduced by an insufficient number of nurse bees, which may reflect a reduced number of prepared brood cells or removal of eggs at a very early stage (Becher et al. 2014).
Eggs: nursing	number of eggs that died today due to lack in available nursing bees
Larvae: nursing	number of larvae that died today due to lack in available nursing bees
Larvae: pollen	number of larvae that died due to lack in protein content of jelly fed by nurse bees today, if actual pollen stores are depleted the protein content of brood food is reduced
Foragers: foraging	number of unsuccessful scouts and successful nectar and pollen foragers that died today due to mortality risk of foraging trips depending on duration of a foraging trip (i.e. for nectar and pollen foragers depending on the distance of the forage patch and the handling time and for scouts on searching time)
Foragers: miles	number of foragers that died today because their total flight distance exceeds 800 km

Table 4: Monthly averages of number of foraging trips per hour (# trips / hour), honey stores (honey (kg)) and percentage of lost foragers due to foraging activities (% forager losses) during summer for the selected forage stress scenarios: nearby foraging (high forage supply at 500 m); distant foraging (high forage supply at 1500 m); high forage supply (at 1000 m foraging distance); low forage supply (at 1000 m foraging distance); June Gap (high forage supply at 1000 m); July Gap (high forage supply at 1000 m); May Gap (high forage supply at 1000 m) and July Gap, low forage (at 1000 m) (mean ± SD, n = 30 per scenario). The single forage patch provided 100 l nectar and 100 kg pollen per day under overall high forage supply, 3 l nectar and 0.5 kg pollen under overall low forage supply.

Scenario	**# trips / hour * 10^3**			**honey (kg)**		**% forager losses**
	July	**Aug.**	**Sep.**	**August**	**Sep.**	**Sep.**
nearby foraging	5.5 ± 1.6	6.2 ± 2.8	4.0 ± 7.7	36.9 ± 3.3	48.3 ± 1.3	2.5 ± 4.8
distant foraging	5.3 ± 1.7	3.4 ± 1.5	2.7 ± 2.4	19.4 ± 1.6	26.7 ± 2.1	4.3 ± 3.8
high forage supply (year 1)	5.8 ± 1.6	5.1 ± 1.7	2.6 ± 4.5	26.0 ± 1.9	37.7 ± 2.1	2.4 ± 4.2
low forage supply (year 1)	5.6 ± 1.2	3.7 ± 1.2	2.5 ± 2.6	20.9 ± 1.6	28.6 ± 1.8	4.5 ± 4.4
high forage supply (year 5)	5.7 ± 1.8	5.7 ± 2.2	2.8 ± 5.1	31.2 ± 3.1	42.5 ± 3.1	2.2 ± 4.1
low forage supply (year 5)	3.4 ± 1.4	2.8 ± 1.2	2.3 ± 2.0	13.0 ± 2.8	18.9 ± 4.1	6.1 ± 5.4
June Gap (year 1)	7.8 ± 2.3	2.5 ± 1.5	1.8 ± 2.3	18.9 ± 2.5	22.0 ± 2.6	4.8 ± 5.3
June Gap (year 2)	4.6 ± 2.2	2.0 ± 1.2	2.1 ± 2.1	13.6 ± 2.9	17.5 ± 4.0	6.0 ± 5.5
July Gap (year 1)	2.8 ± 1.6	2.9 ± 1.3	2.8 ± 2.6	16.5 ± 2.1	23.5 ± 2.4	5.2 ± 4.5
July Gap (year 2)	2.2 ± 1.2	2.3 ± 1.2	2.3 ± 2.1	12.2 ± 2.5	17.4 ± 3.8	6.5 ± 5.7
May Gap (year 1)	5.5 ± 1.4	4.0 ± 1.5	2.9 ± 3.8	21.9 ± 2.0	32.5 ± 2.3	3.4 ± 4.3
May Gap (year 2)	5.5 ± 1.5	4.1 ± 1.5	2.9 ± 3.9	22.1 ± 2.7	33.1 ± 3.4	3.4 ± 4.3
July Gap, low forage (year 1)	6.7 ± 2.1	1.8 ± 1.0	1.9 ± 1.4	11.6 ± 1.3	14.0 ± 1.9	7.2 ± 6.0
July Gap, low forage (year 2)	3.0 ± 1.6	1.1 ± 0.9	1.2 ± 1.0	5.8 ± 1.9	7.1 ± 2.9	7.4 ± 8.0

Figure Legends

Figure 1: **Proportions of colonies that died (overview of all simulations):** Exploration of colony losses after five years depending on the four investigated forage stressors acting alone or in combination: foraging distance (500, 1000 or 1500 meters); forage supply (high or low forage supply); timing of induced forage gap (month: none, April, May, June, July, August or September) and duration of induced forage gap in the respective month in days (none, 6, 15, 21 or 30). For each stressor combination the percentage of colony losses of 30 simulated colonies after 5 years is indicated by the grayscale: white (< 10 %), light grey (10 – 25 %), grey (26 – 50 %), dark grey (51 – 80 %) and black (> 80 %).

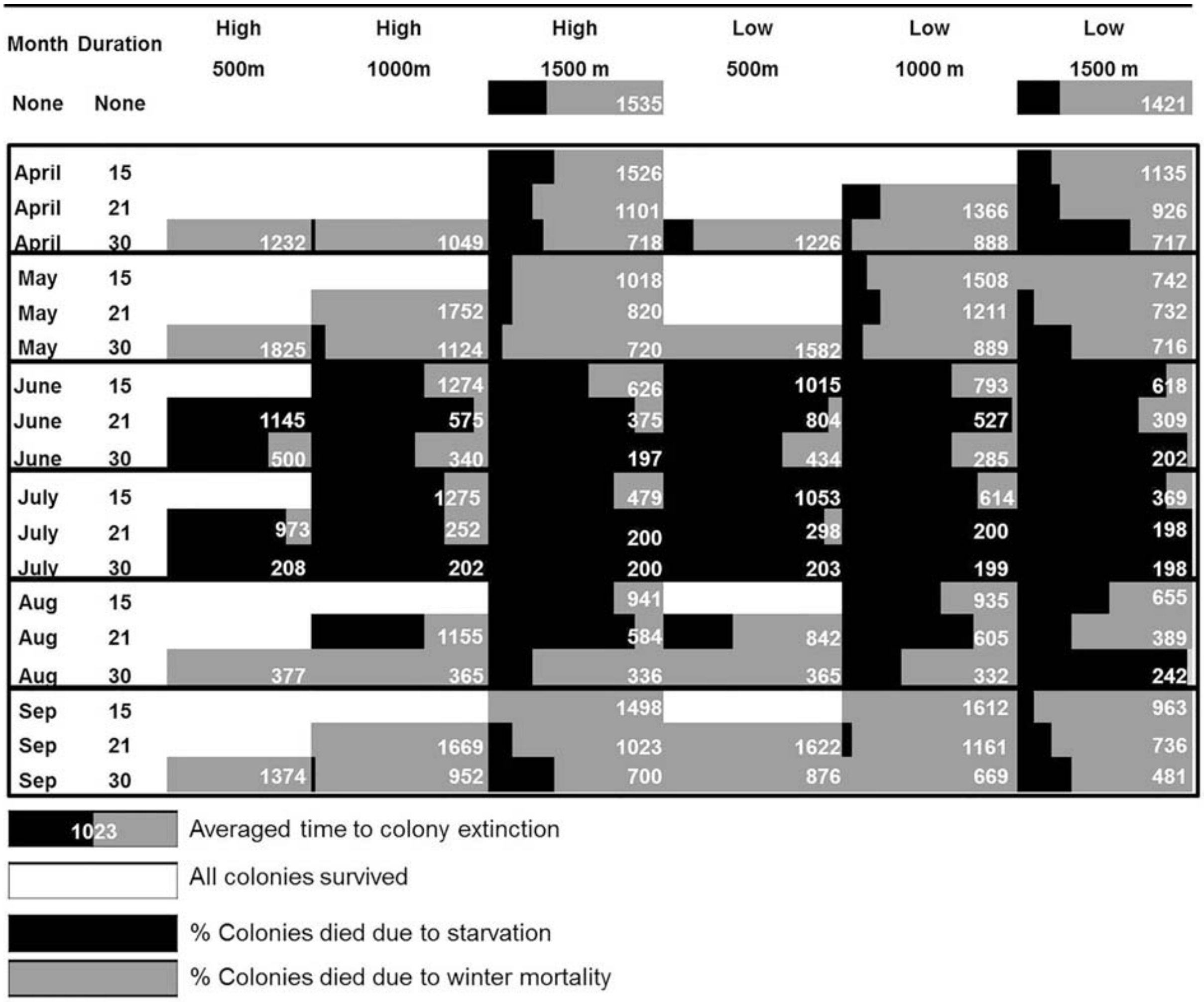


Month	Duration	High 500m	High 1000m	High 1500m	Low 500m	Low 1000m	Low 1500m
None	None	□	□	░	□	□	■
April	6	□	□	▓	□	□	■
April	15	□	□	▓	□	□	■
April	21	□	□	■	□	░	■
April	30	░	■	■	▓	■	■
May	6	□	□	▒	□	□	■
May	15	□	□	■	□	■	■
May	21	□	▒	■	□	■	■
May	30	□	■	■	▓	■	■
June	6	□	□	■	□	░	■
June	15	□	■	■	░	■	■
June	21	□	■	■	■	■	■
June	30	■	■	■	■	■	■
July	6	□	□	▒	□	□	■
July	15	□	▓	■	▒	■	■
July	21	■	■	■	■	■	■
July	30	■	■	■	■	■	■
Aug	6	□	□	■	□	■	■
Aug	15	□	□	■	□	■	■
Aug	21	■	■	■	■	■	■
Aug	30	■	■	■	■	■	■
Sep	6	□	□	▓	□	▓	■
Sep	15	□	□	■	□	▓	■
Sep	21	□	░	■	▒	■	■
Sep	30	▓	■	■	■	■	■

Colony losses after 5 years

□	< 10 %
░	10 – 25 %
▒	26 – 50 %
▓	51 – 80 %
■	> 80 %

Figure 2: Timing and reason of colony extinction (overview, all simulations): Average time to colony extinction and probability of colony extinction due to winter mortality or starvation depending on the four forage stressors acting alone or in combination (settings as described in Fig. 1): foraging distance (500, 1000 or 1500 meters); forage supply (high or low forage supply); timing of induced forage gap (month: none, April, May, June, July, August or September) and forage gap duration in the respective month given in days (none, 15, 21 or 30). For each stressor combination the average time to colony extinction is indicated by white numbers within black- and grey-colored cells. Empty cells indicate that none of the simulated colonies were lost within five years, colored cells show the probability of starvation in summer (black bar) and winter mortality (grey bar). Colony extinction due to starvation was defined as occurring if honey stores were completely exhausted, resulting in the immediate death of all brood and adult bee stages. Colony extinction due to winter mortality was defined as occurring when the colony size was below the critical threshold (4000) at the end of a year.



Month	Duration	High 500m	High 1000m	High 1500 m	Low 500m	Low 1000 m	Low 1500 m
None	None			1535			1421
April	15			1526			1135
April	21			1101		1366	926
April	30	1232	1049	718	1226	888	717
May	15			1018		1508	742
May	21		1752	820		1211	732
May	30	1825	1124	720	1582	889	716
June	15		1274	626	1015	793	618
June	21	1145	575	375	804	527	309
June	30	500	340	197	434	285	202
July	15		1275	479	1053	614	369
July	21	973	252	200	298	200	198
July	30	208	202	200	203	199	198
Aug	15			941		935	655
Aug	21		1155	584	842	605	389
Aug	30	377	365	336	365	332	242
Sep	15			1498		1612	963
Sep	21		1669	1023	1622	1161	736
Sep	30	1374	952	700	876	669	481

1023	Averaged time to colony extinction
☐	All colonies survived
■	% Colonies died due to starvation
▨	% Colonies died due to winter mortality

Figure 3: Variation partitioning in **(A)** colony extinction after five years, **(B)** colony extinction due to starvation, and **(C)** time to colony extinction among the explanatory stress factors foraging distance, timing of induced forage gap and duration of a forage gap, and their interactions. Forage supply and its interactions were excluded from variation partitioning, because it occurred rarest in the subset of the best models as identified with AIC.

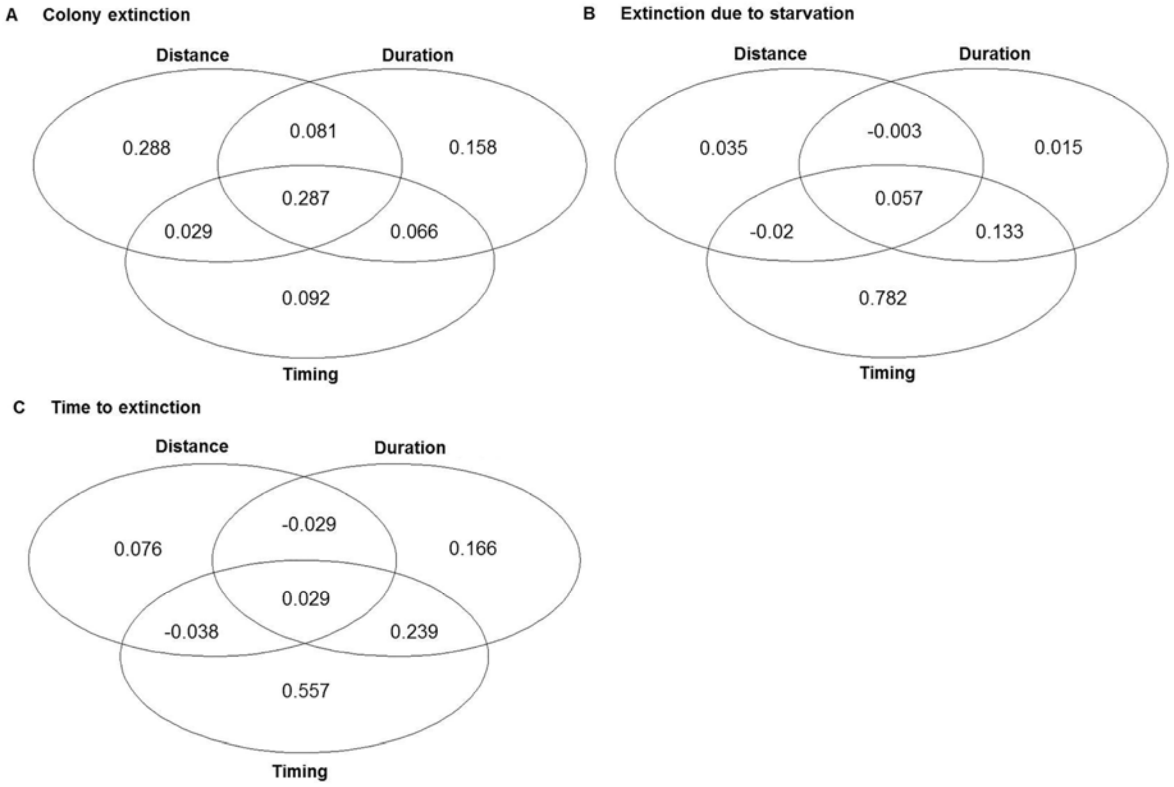


Figure 4: Foraging distance (high; no gaps): Consequences of increased foraging distance on colony dynamics assuming high forage supply and no forage gaps. Foraging trips are possible between day 80 (mid-March) and day 290 (mid-October). **(A)** Mean number of worker bees over time for nearby foraging (500 m, black line) and distant foraging (1500 m, grey line) for a time period of five years (1825 days). The mean is taken over surviving colonies only. Error bars are shown for every sixtieth day (mean ± SD, n = 30). (**B**) and (**C**): Mortality of brood stages and foragers in terms of mean number of dead individuals or eggs that were not laid because the queen had to reduce egg-laying (n = 30) for nearby **(B)** and distant foraging **(C)** are shown for the first year of simulation. Under distant foraging the second peak of eggs not laid (black line) in June and losses of eggs (black dotted line) and larvae (grey dotted line) due to lack in available nurse bees was much higher compared to nearby.

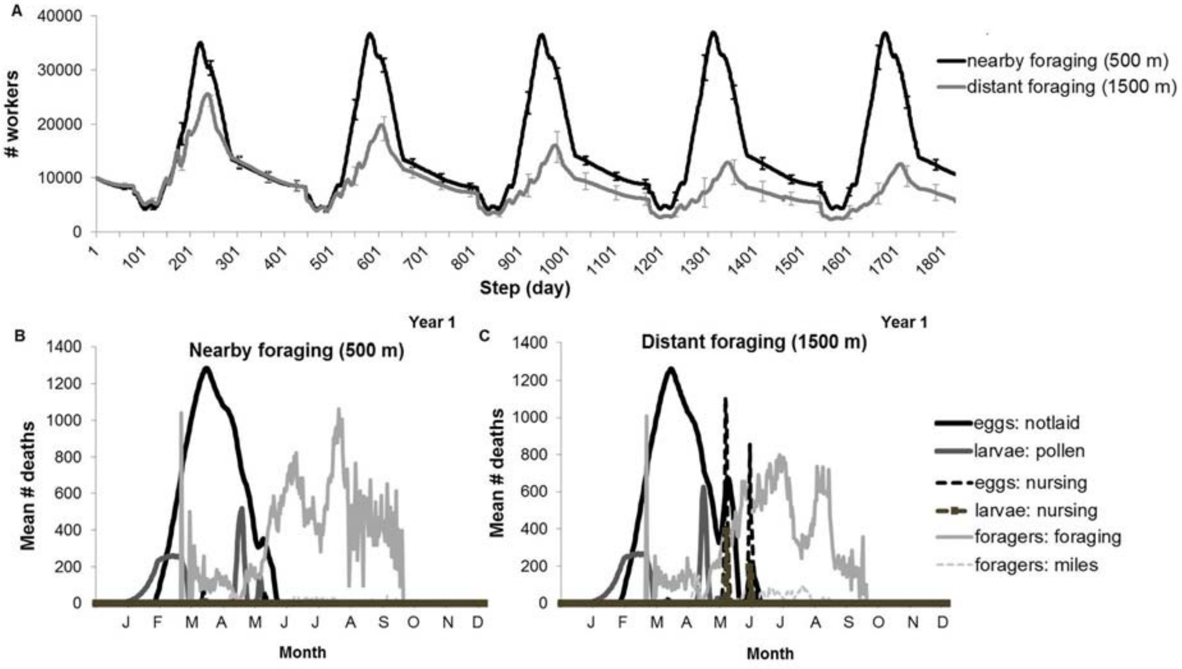


Figure 5: Forage supply (1000 m; no gaps): (A) The effect of high forage supply (100 L nectar and 100 kg pollen per day, black line) and low forage supply (3 L nectar and 0.5 kg pollen per day, grey line) on averaged number of workers is shown for a time period of five years (1825 days). The mean number of workers is based on surviving colonies only, error bars are shown for every sixtieth day (n = 30). Mortalities of brood stages and foragers in terms of mean number of dead individuals (n = 30) for high forage supply **(B)** and low forage supply **(C)** are shown for the fifth year. Foraging trips are possible between day 80 (mid-March) and day 290 (mid-October).

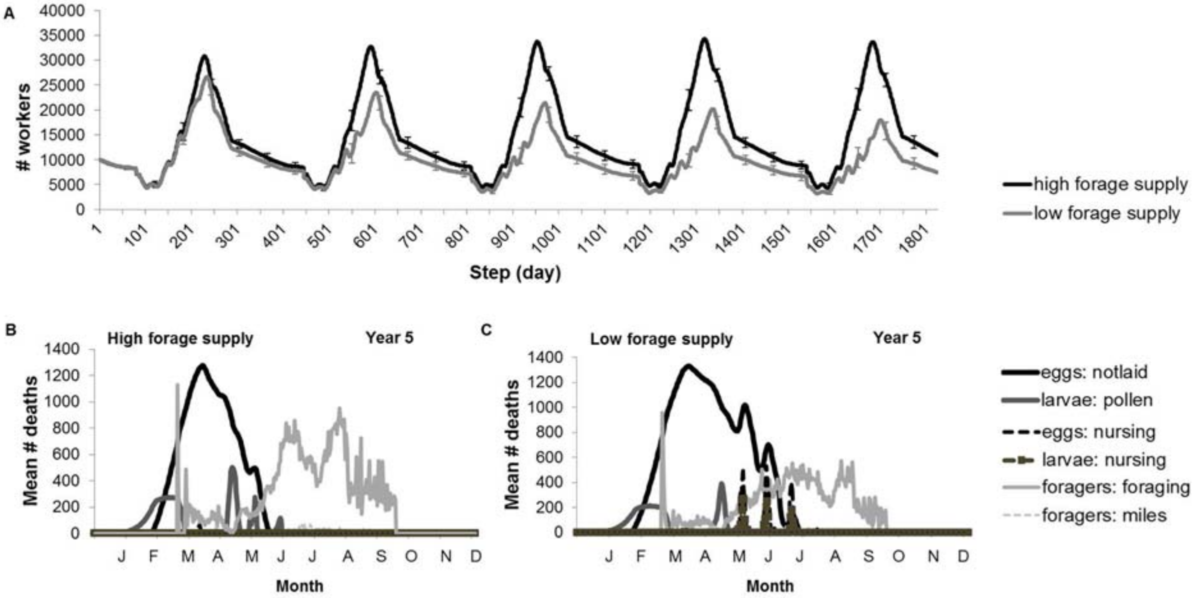


Figure 6: Foraging distance and forage supply (no gaps): The monthly averages of colony size **(A and B)**, honey stores **(C and D)** and foraging trips per hour multiplied by 10³ **(E and F)** from June to September in the first (left panels) and the fifth year (right panels) of simulation for the different combinations of forage supply and foraging distance.

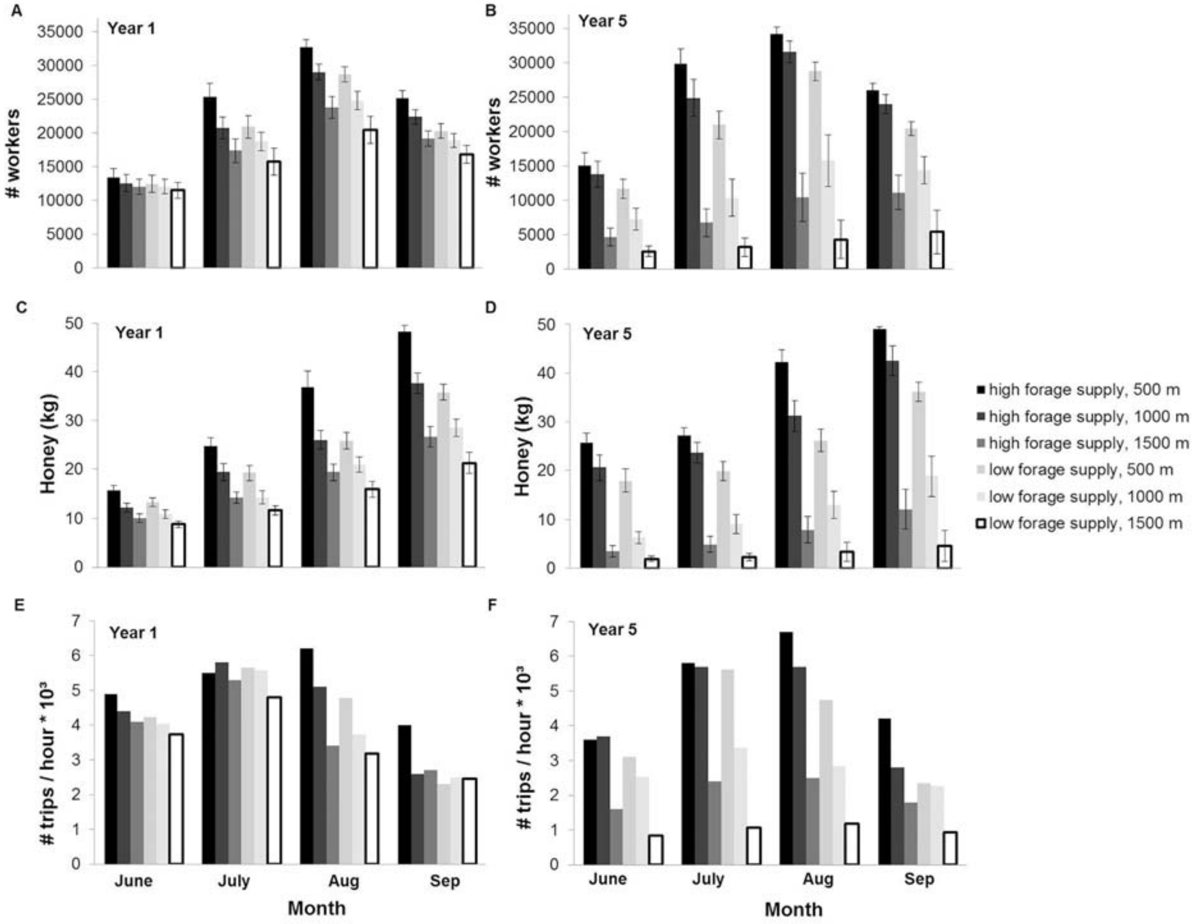


Figure 7: Foraging distance and forage supply (no gaps): Comparison of mortalities under stress to most favourable foraging settings (high forage supply, 500 m; zero line) in June and July of the first (left column) and fifth year (right column). **(A and B)** Difference between potential and actual number of eggs laid (Δ # eggs: not laid), **(C and D)** differences in number of eggs that died due to insufficient number of available nurse bees (Δ # eggs: nursing), and **(E and F)** the difference in number of larvae that died due to insufficient number of nurse bees (Δ # larvae: nursing). Differences shown are the average of 30 simulations per scenario.

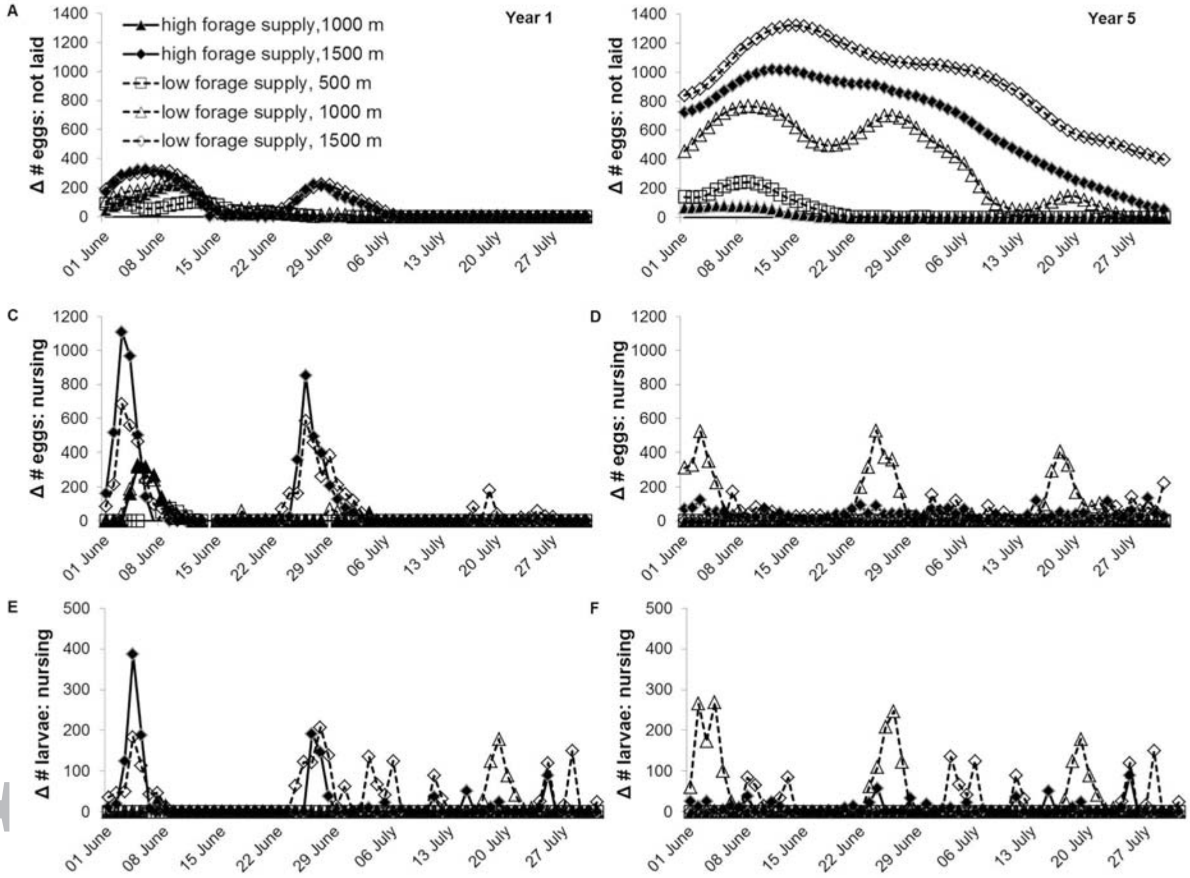


Figure 8: Forage supply and timing foraging gap (1000m, 15d gap): Effects of 15 day forage gaps on colony dynamics. Foraging distance was intermediate (1000m). During a forage gap forage availability was set to zero but constant weather conditions did not restrict searching trips. A forage gap started always on the first day of a given month and was explored for each month separately. **(A)** The impact of a 15 day forage gap induced in May (black line), June (grey line), or in July (black dashed line) under high forage supply, and a 15 day forage gap induced in July under low forage supply (grey dashed line) on the average number of workers for five years is shown. The mean number of workers is based on surviving colonies only, error bars are shown for every sixtieth day (n = 30). The monthly averages of honey stores **(B and C)** and foraging trips per hour multiplied by 10³ **(D and E)** from June to September in the first (left panels) and the second year (right panels) of simulation are shown for gaps in May (high supply), June (high supply), and July low and high forage supply).

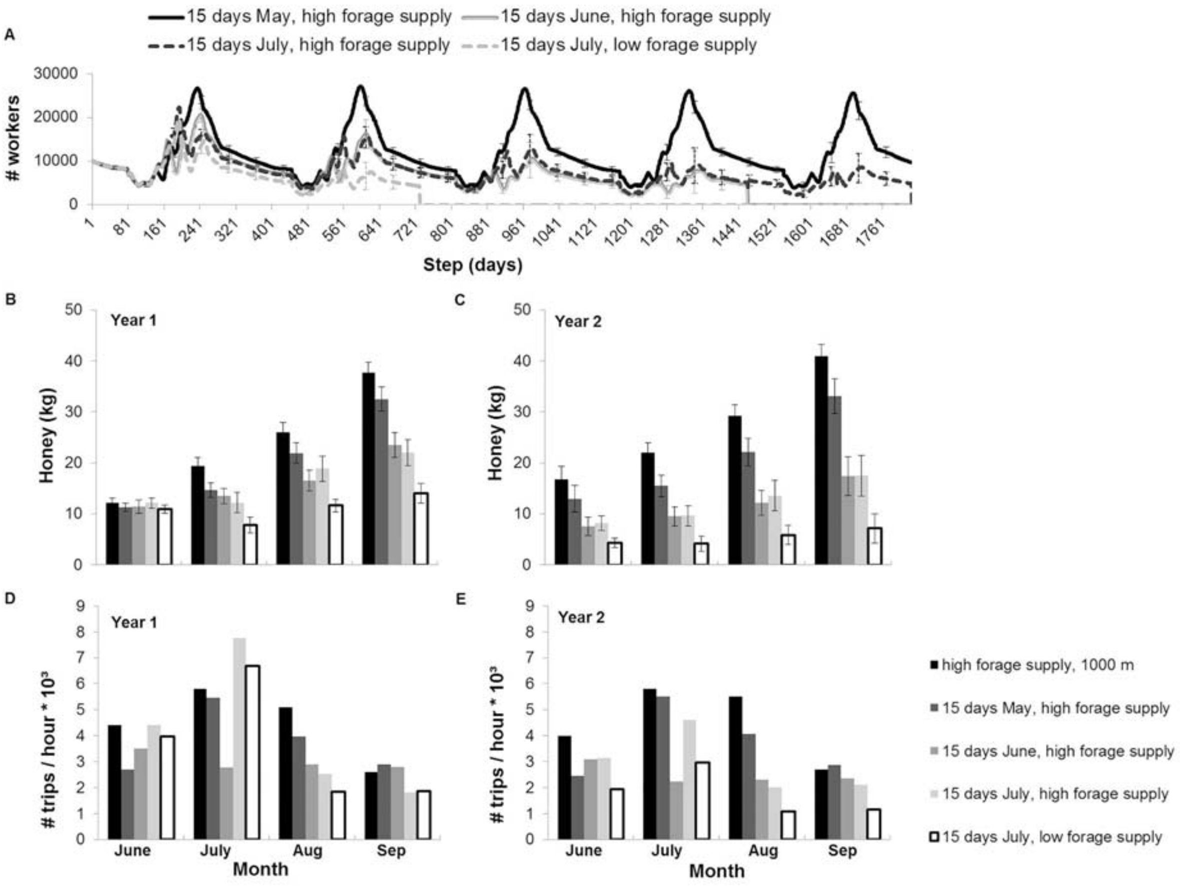


Figure 9: Forage supply and timing foraging gap (1000m, 15d gap): Effects of 15 day forage gaps on mortalities of brood stages in June and July of the first and second year compared with the most favourable forage (no gap) scenario (high forage supply, 1000 m; zero line) are shown. Foraging distance was 1000 m. All forage gap settings were as for Fig 8. **(A and B)** Difference between potential and actual number of eggs laid (Δ # eggs: not laid); **(C and D)** differences in number of larvae that died due to lack in protein content of jelly fed by nurse bees (related to pollen foraging; Δ # larvae: pollen) are illustrated. Mortalities shown are mean numbers of dead individuals (n = 30 per combination).