RESULTS

This section presents the outcomes of the simulation and numerical experiments conducted with the proposed model. The results are depicted graphically to enhance clarity and aid visualization.

For the first result of inter-colony dynamics, we incorporated the drifting behaviour of honeybees into the model of the two healthy colonies. The parameters $d_n = 0.003$, $\gamma_n = 0.7$, and $r_n = 0.64$ for all $n = 1,2$ is incorporated and the results are shown in the figure below.

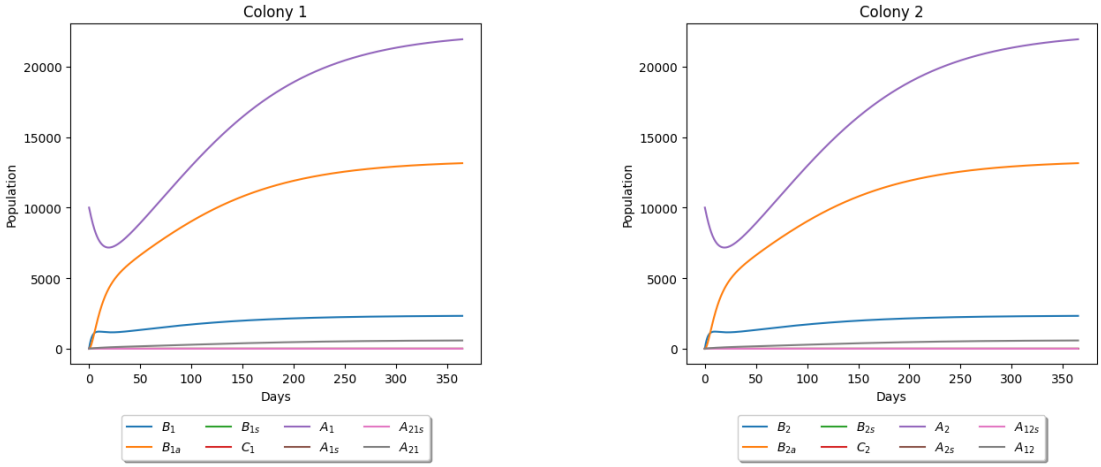

Figure 1. Dynamics of Two Healthy Colonies with Drifting Behavior. The parameters used are in **Error! Reference source not found.**. The initial conditions are also $(\mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{10000}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{10000}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0})$ indicating that both are healthy.

The graph illustrated that when drifting occurs, the behavior of the colonies remains largely similar to when there is no drifting, albeit with the addition of foreign bees to the colony dynamics. Notably, there is only a marginal difference in the population of the original bees within the colony, but this is accompanied by the addition of the population of foreign bees. Based on the findings from **Figure 1**, we can also determine the percentage of honeybees that have drifted from the other colony, as further illustrated in **Figure 2**.

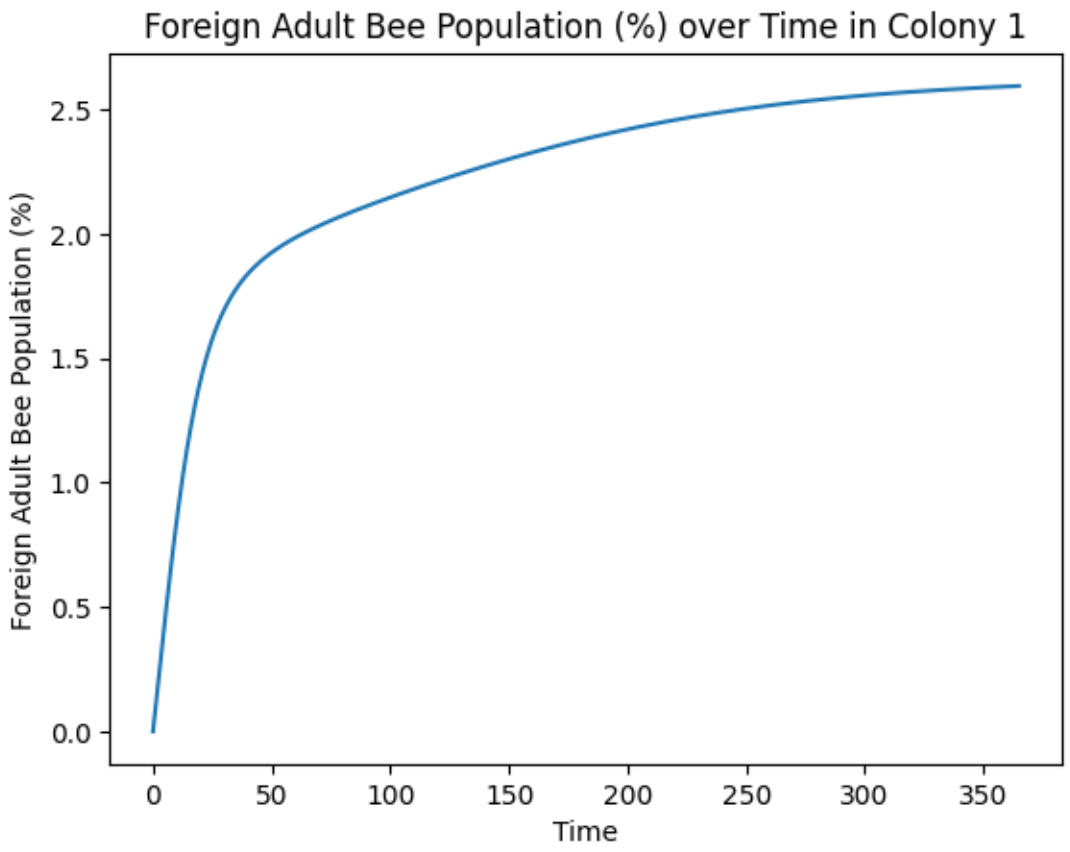

Figure 2. Percentage of drifted honeybees over time. This example from Colony 1 demonstrates behavior similar to that of Colony 2, as evidenced by the results in **Figure 1**. Therefore, we presented the results for Colony 1, recognizing their equivalence to those of Colony 2.

To further analyze the impact of drifting on the colony, we varied the drifting rate by adjusting the parameter d_n as detailed in Error! Reference source not found.. Specifically, we conducted 10 simulations with drifting rates ranging from 1% ($d_n = 0.003$) to 100% ($d_n = 0.3$) for a healthy Colony 1. The resulting effects are depicted in **Figure 3**.

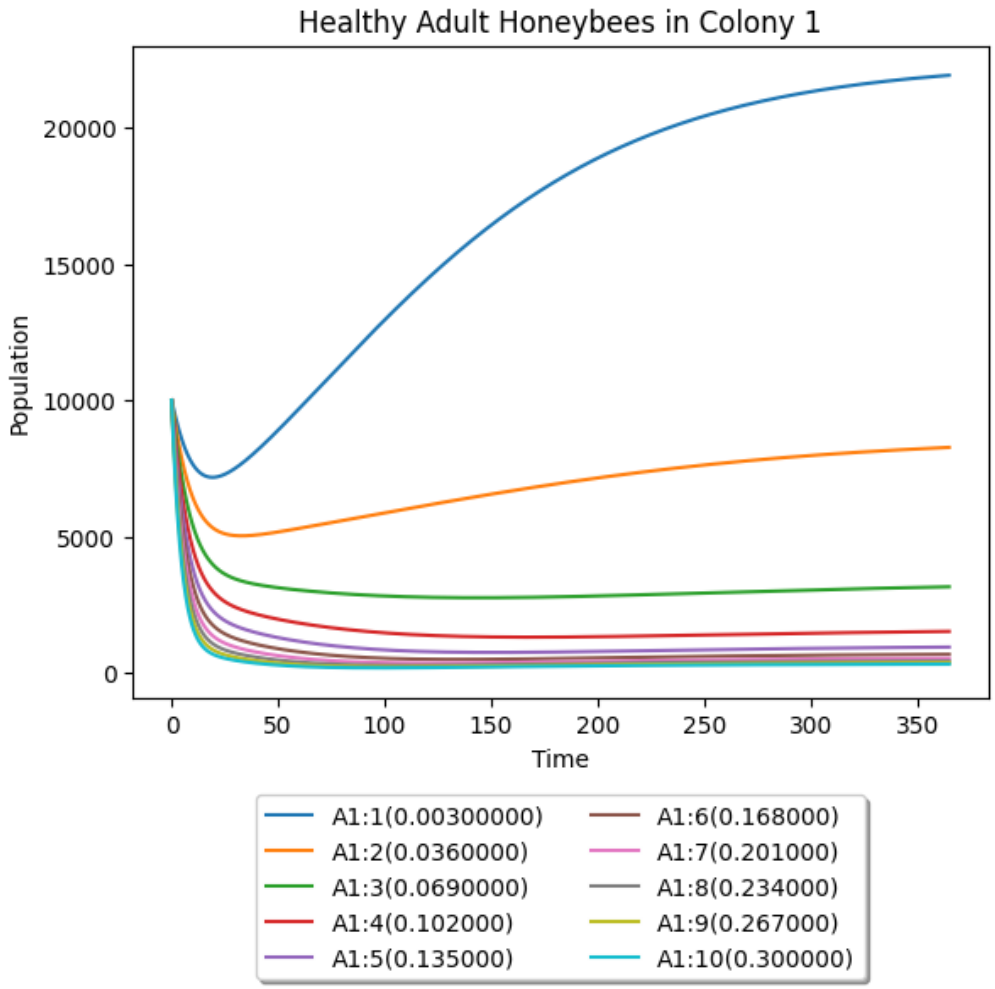

Figure 3. Effects of different values of drift rate to the healthy Colony 1.

From the graph above, we observed that as the drifting rate increases for a healthy Colony 1, it may result in a weakened colony, potentially leading to collapse, particularly at higher drift rates.

Now, we delved deeper into studying the parameters influencing the dynamics of a healthy colony in drifting. In the following heatmap, we varied both the drifting rates, d_1 and d_2, of the two colonies.

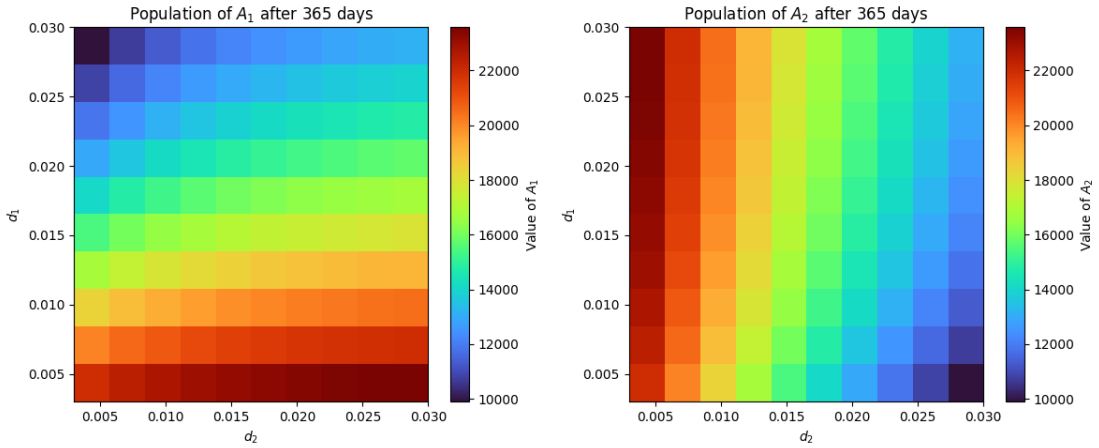

Figure 4. Dynamics of adult honeybees in two healthy colonies with varied drifting rates

The heatmap above illustrated the outcomes for the adult honey bee populations of Colony 1 and Colony 2, indicating whether they will survive or collapse as both their drifting rates are varied. From this analysis, we can conclude that both colonies will survive regardless of whether drifting is at 0% or 100%, as long as the percentage of forager bees (honeybees of an appropriate age capable of leaving the colony) in both colonies remains at 30%. If we include varying the percentage of forager bees and expand the range of d_n from 0% to 100%, the resulting heatmap is displayed below.

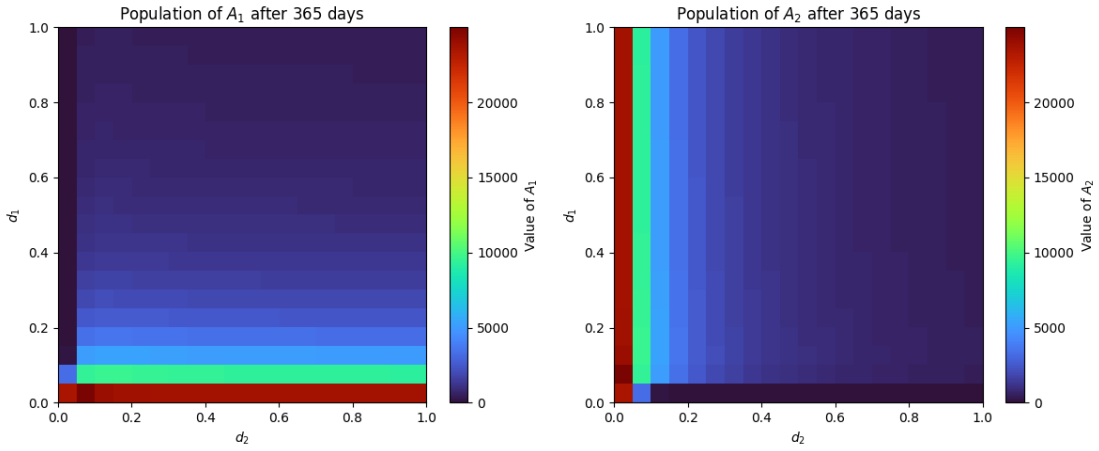

Figure 5. Dynamics of two colonies with varied drifting rates including the percentage of forager honeybees.

From the heatmap, we can identify points where colony collapse occurs. While there isn't a specific percentage of the total population that guarantees collapse, as colony losses are less frequently associated with collapse [**Error! Reference source not found.**], we can set collapse as occurring when the percentage

of the current population to the original initial population is less than 1% (1000). In the heatmap, areas with a deeper blue color indicate collapse.

Additionally, we analyzed the combined effects of drift rate d_n and return rate r_n on Colony 2 to determine whether it will survive or collapse under varied parameters. By varying d_n and r_n and plotting this in a heatmap, it can visualize how these two parameters interact and influence each other within the context of honeybee behavior and colony dynamics. Their potential implications are:

- High d_n, Low r_n: This scenario suggests high levels of drift, where bees frequently leave their original colony but successfully integrate into new colonies. This could be due to weak guarding behavior in the receiving colony or aggression from resident bees, leading to the drifting bees either dying or becoming lost outside the two-colony system.
- Low d_n, High r_n: Here, while bees may initially show less inclination to drift, those that do are unsuccessful at integrating into other colonies. This may imply a less hospitable environment outside or strong guarding behavior by the receiving colony.
- High d_n, High r_n: This combination could indicate a dynamic in which bees frequently drift but struggle to integrate into new colonies, possibly suggesting an unhealthy colony or an inhospitable network of colonies.
- Low d_n, Low r_n: This scenario may suggest a stable colony environment with minimal drifting and few bees returning to their original colony, indicative of a well-connected network of colonies.

In the following figure, we analyzed the effect of varying both the drift rate d_n and return rate r_n in Colony 2.

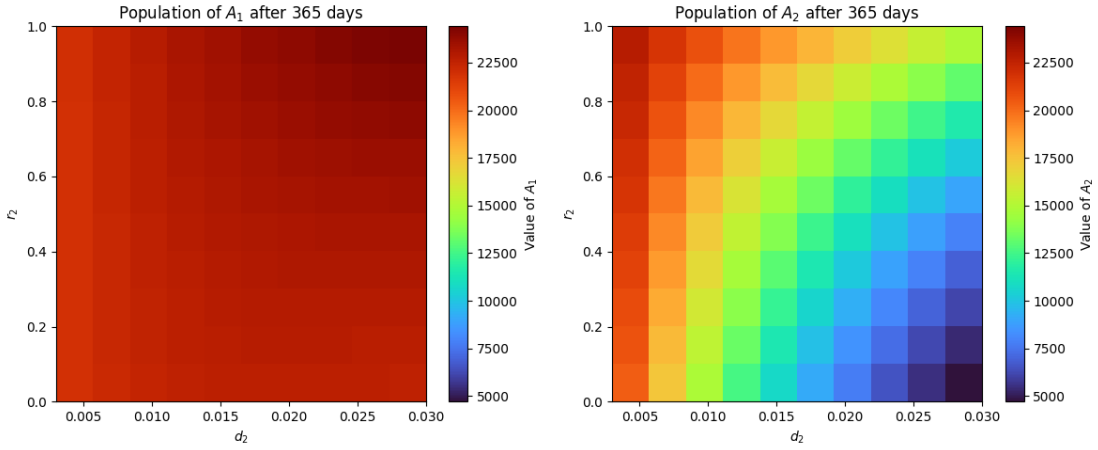

Figure 6. Effect of varying drift rate and return rate to the survival of the adult honeybees.

From the heatmap shown in **Figure 6**, we can see that adult honeybees in Colony 2 still survived, however it became weak, even when there is no return rate ($r_n = 0$) and has high drift rate ($d_n = 0.03$) in Colony 2. The colony survival under these parameter values is further illustrated in the figure below.

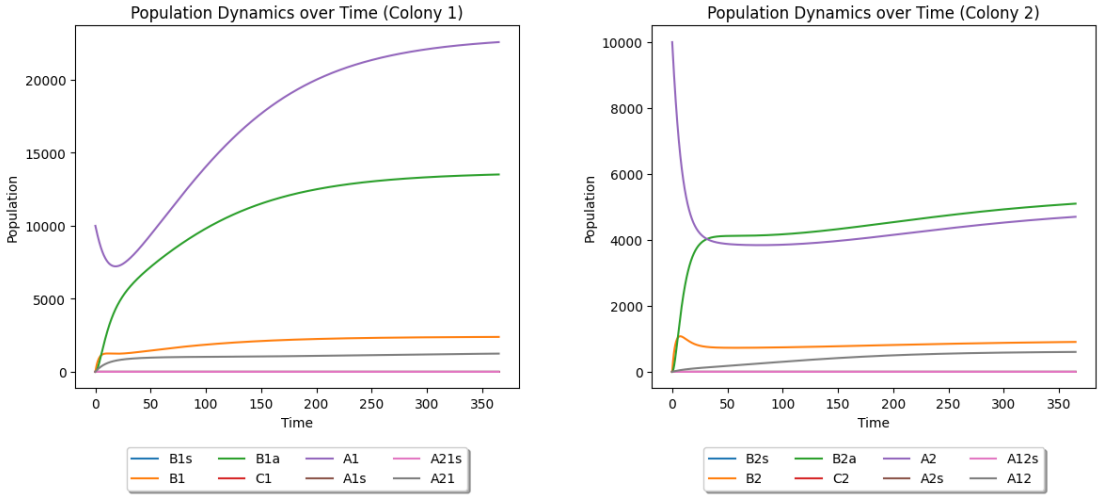

Figure 7. Inter-colony dynamics of the two healthy colony when $r_n = 0$ and $d_n = 0.03$ on Colony 2.

Finally, in this scenario, if we also vary the percentage of foragers and expand the range of d_n from 0% to 100%, the survival of Colony 2 is depicted in the figure below.

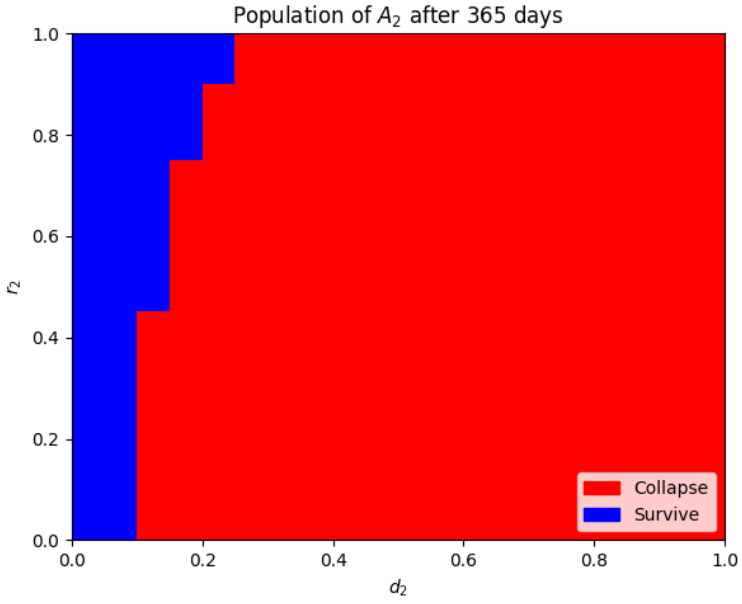

Figure 8. Colony 2 survival heatmap.

We can further explore various combinations of parameters to examine the survival or collapse of a healthy colony. However, we will now shift our focus to the primary objective of this study, which involves integrating AFB infection into the inter-colony dynamics. For the first simulation involving the AFB infection, we started by adding an infected adult to Colony 2. The results are shown in **Figure 9**.

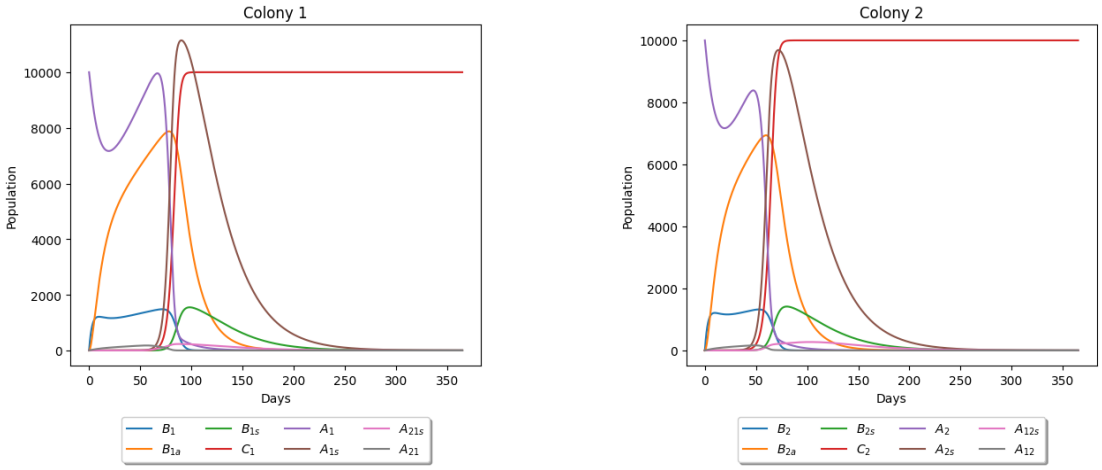

Figure 9. Dynamics of the two colonies with drifting infected adult honeybee from Colony 2. The parameters used here is also in **Error! Reference source not found.**. The initial conditions are $(\mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{10000}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{10000}, \mathbf{1}, \mathbf{0}, \mathbf{0}, \mathbf{0}, \mathbf{0})$, indicating the presence of an infected adult in Colony 2.

From the graphs above, it is evident that both colonies experience mortality between 250 to 300 days after the infection begins in Colony 2. Interestingly, despite the infection originating in Colony 2, the number of infected adult honeybees in Colony 1 peaks higher than that of Colony 2 over time, potentially increasing the risk of spreading the infection to other colonies when a portion of infected bees in Colony 1 drift to neighboring colonies beyond the two-colony system in the model. This result aligns with findings from Betti et al.'s paper [3], where the second colony in their study peaks slightly higher than the source colony. However, the peak we observed is more pronounced. Lastly, our results from Berkeley Madonna suggested that drifting may actually help decrease the spread of infection in both colonies compared to when there is no drifting. This finding exhibits a degree of consistency with the outcomes documented by Betti et al. [**Error! Reference source not found.**]. The results we got from Berkeley Madonna are summarized in the table below.

Table 1. Day of First Brood Infection Onset.

Scenario	**Days of First Brood Infection**	
	Colony 1	**Colony 2**

Infection without drifting (Intra-colony)	38.9 days	38.9 days
Infection started in one colony (Colony 2) with drifting at **1% on both colonies** ($d_n =$ 0.003)	59.44 days	39.16 days
Infection started in one colony (Colony 2) with drifting at **10% on both colonies** ($d_n =$ 0.03)	53.98 days	41.54 days
Infection started in one colony (Colony 2) with drifting at **50% on both colonies** ($d_n =$ 0.15)	56.34 days	50.2 days
Infection started in one colony (Colony 2) with drifting at **10% on Colony 2** ($d_2 =$ 0.03)	48.68 days	44.94 days
Infection started in one colony (Colony 2) with drifting at 5**0% on Colony 2** ($d_2 =$ 0.15)	40.88 days	105.72 days
Infection started on both colonies with drifting at **1% on both colonies** ($d_n =$ 0.003)	39.14 days	39.14 days
Infection started on both colonies with drifting at **10% on both colonies** ($d_n =$ 0.03)	41.32 days	41.32 days
Infection started on both colonies with drifting at 5**0% on both colonies** ($d_n =$ 0.15)	48.78 days	48.78 days

We further explored intriguing scenarios, such as when Colony 2 is weaker than Colony 1, resulting in notable outcomes depicted in **Figure 10**.

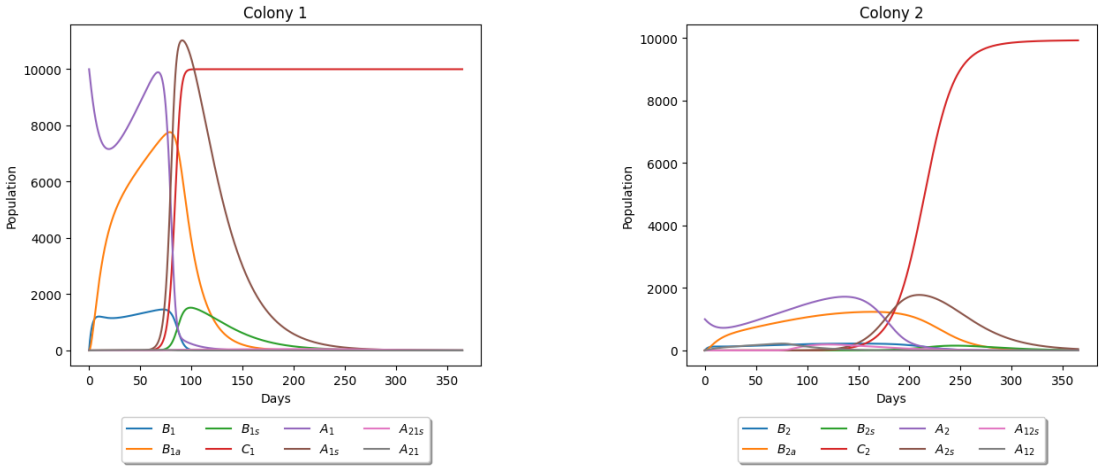

Figure 10. Dynamics of the two colonies with drifting infected adult honeybee from a weak Colony 2. Here, we set $\boldsymbol{L_2 = 150}$ and $\boldsymbol{w_2 = 2100}$. We also set the initial value of $\boldsymbol{A_2 = 1000}$ so that we weaken the Colony 2.

From the results, we observed that despite Colony 2 having the initial infected adult, Colony 1 is the first to collapse. This suggests that higher population density may accelerate the spread of AFB transmission within a colony. Further studies could explore whether population density serves as a critical factor in transmission dynamics.

We further investigated the dynamics using the model by varying important parameters that are likely to impact the trajectory of the system. Our initial exploration involves varying the parameter α_2, which is detailed in Error! Reference source not found., to observe its effects on the colony dynamics of both colonies, particularly with an infected adult honeybee present in Colony 2. The results are shown below.

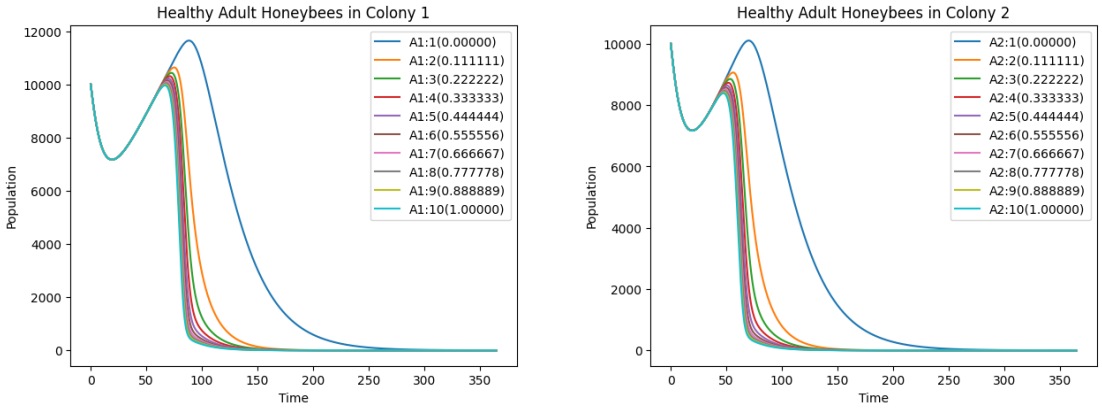

Figure 11. Effect of varying α_2 on adult honeybee dynamics with infected adult in Colony 2.

From the graphs depicted in **Figure 11**, we can see that for all values of α_2 from [0,1], the effect of α_2 does not help much on the colony survival, specifically the adult honeybee population.

Now, let's examine its impact on the brood infection within the system. We can see the results in the following figure below.

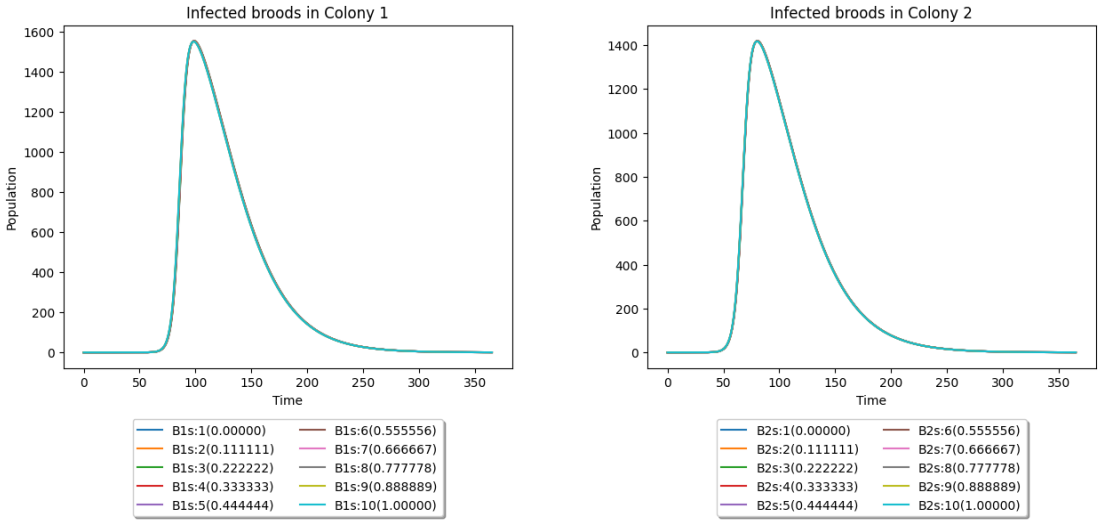

Figure 12. Effect of varying α_2 on brood dynamics with infected adult in Colony 2.

From the results above, it's evident that varying α_2 does not significantly influence the brood dynamics.

Next, we explored other infection rates for adult honeybees, like α_3. Similar to α_2, α_3 represents the rate at which adult bees become infected. The following figure showed how varying α_3 affects the adult honeybee population.

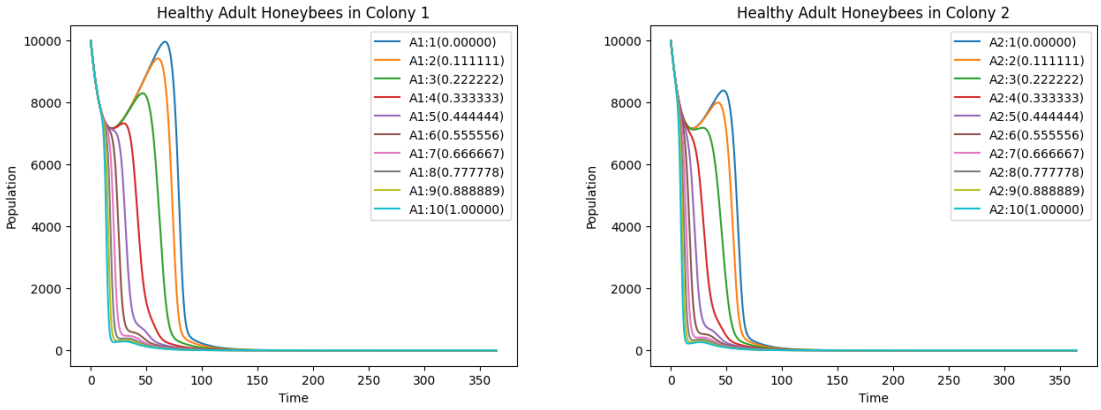

Figure 13. Effects of varying α_3 on adult honeybee dynamics with infected adult in Colony 2.

From **Figure 13**, any values from the batch runs ranging [0,1] does not affect much on colony survival. It is observed that increasing values up to 1 only prolong the lifespan of adult honeybees before eventual mortality.

We further investigated the effect of varying α_3 into the brood infection now. The results can be seen from the figure below.

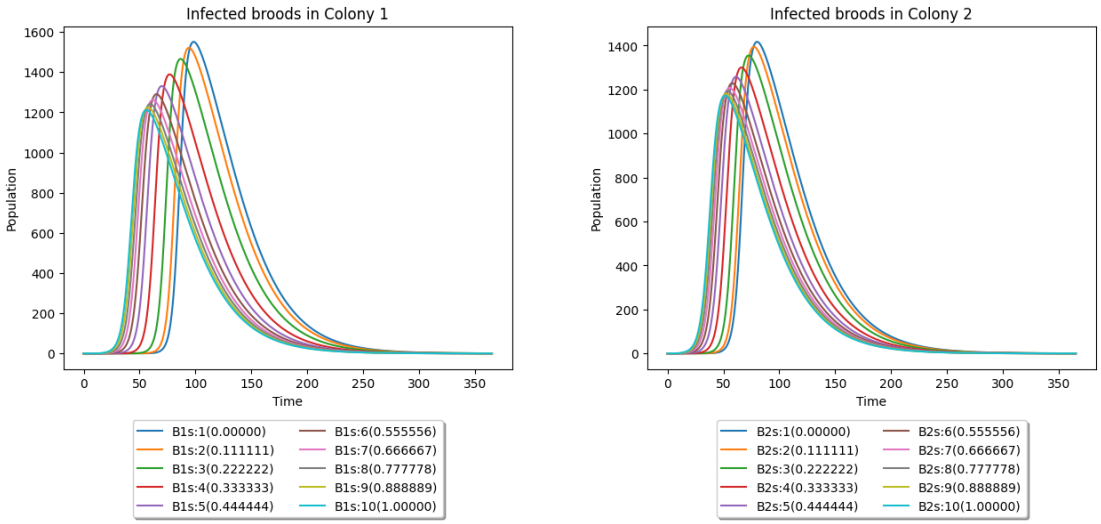

Figure 14. Effect of varying α_3 on brood dynamics with infected adult in Colony 2.

Based on the data presented in the figure above, it is apparent that infected broods will succumb to the infection across all values of α_3 within the range of [0,1]. Lower values of the parameter merely delay the eventual mortality of the infected broods.

Next, we explore another parameter related to infection rates: α_1. Like the previous parameters, α_1 represents an infection rate, specifically concerning broods. We conducted experiments by varying α_1, and the findings are presented below.

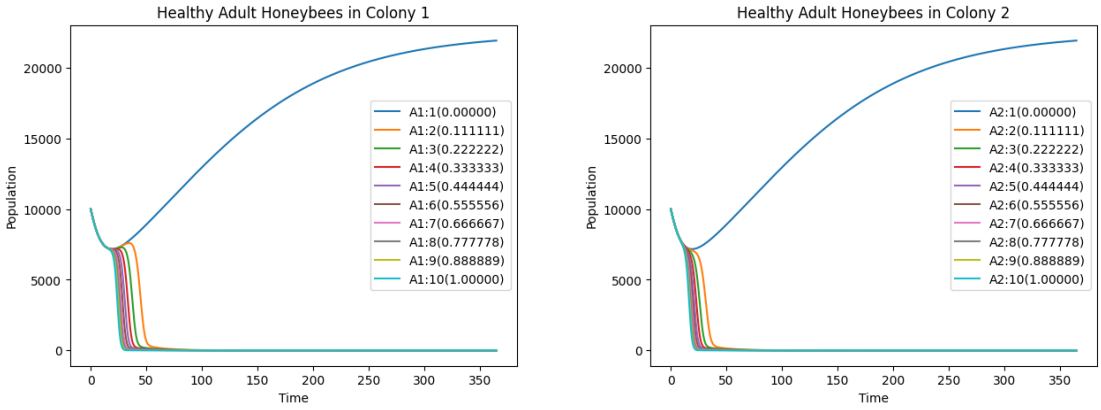

Figure 15. Effects of varying α_1 on adult honeybee dynamics with infected adult in Colony 2.

The findings from the graphs show a significant shift from the previous two parameters. We now observe a potential for adult honeybee survival when parameter α_1 is zero. Because of this, it is intriguing to also see what will happen to the brood dynamics. We can see the results from the following figure.

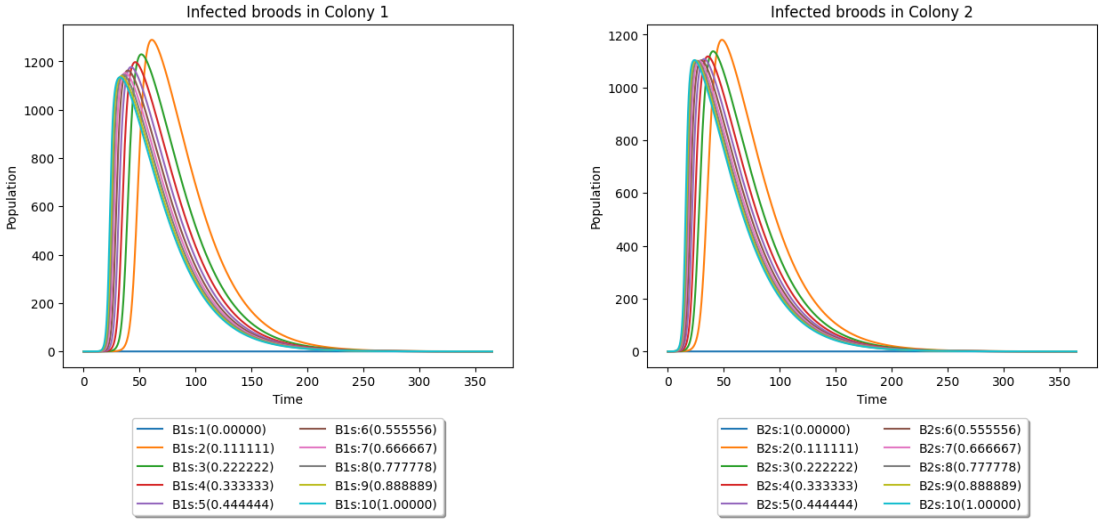

Figure 16. Effect of varying α_1 on brood dynamics with infected adult in Colony 2.

Correlating with the survival of adult honeybees, a notable observation arises when parameter $\alpha_1 = 0$, despite not being immediately apparent due to the graph displaying a flat line at 0. Both colonies in this scenario (varying α_1) exhibit survival without any infections. This finding holds significant implications, suggesting the critical importance of the infection rate among broods for colony survival and health. Consequently, it can be inferred that infected broods may constitute a more decisive factor in colony health and survival than infected adult honeybees. Further studies into these results is warranted.

Moving on from the infection rates parameters, we also studied the effects of varying γ_2 on the adult honeybee population, which is the rejection rate of drifting honeybees from Colony 2 that are not accepted by the receiving colony, as discussed in Error! Reference source not found.. The results are shown below.

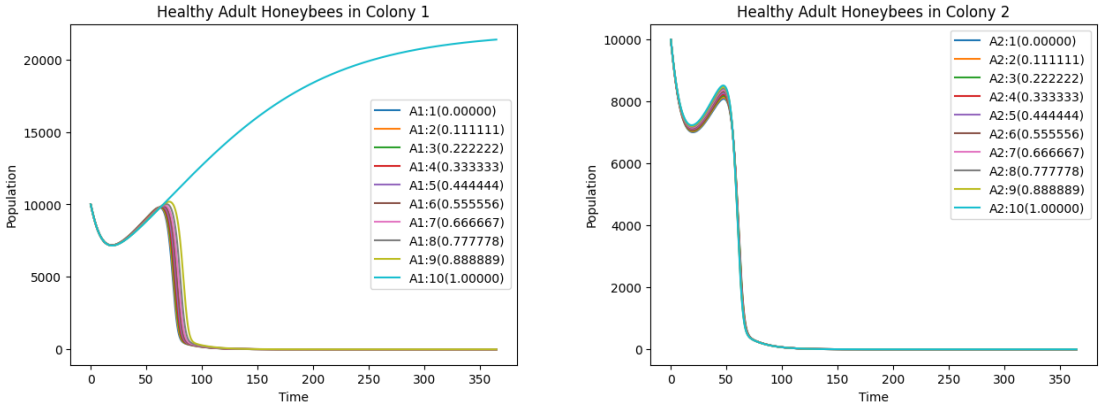

Figure 17. Effects of varying γ_2 on adult honeybee dynamics with infected adult in Colony 2.

Based on the findings depicted in **Figure 17**, when Colony 1 consistently rejects all drifting adult honeybees from Colony 2, Colony 1 can survive without experiencing infection within its colony. Conversely Colony 2, where AFB infection initially originated, will still face colony collapse due to the presence of the disease.

Additionally, we investigated another parameter, φ_1, by conducting 10 batch runs to observe the effects of varying the rate at which diseased dead brood is cleaned by adult bees on the onset of the first brood infection. The results of these experiments are presented below.

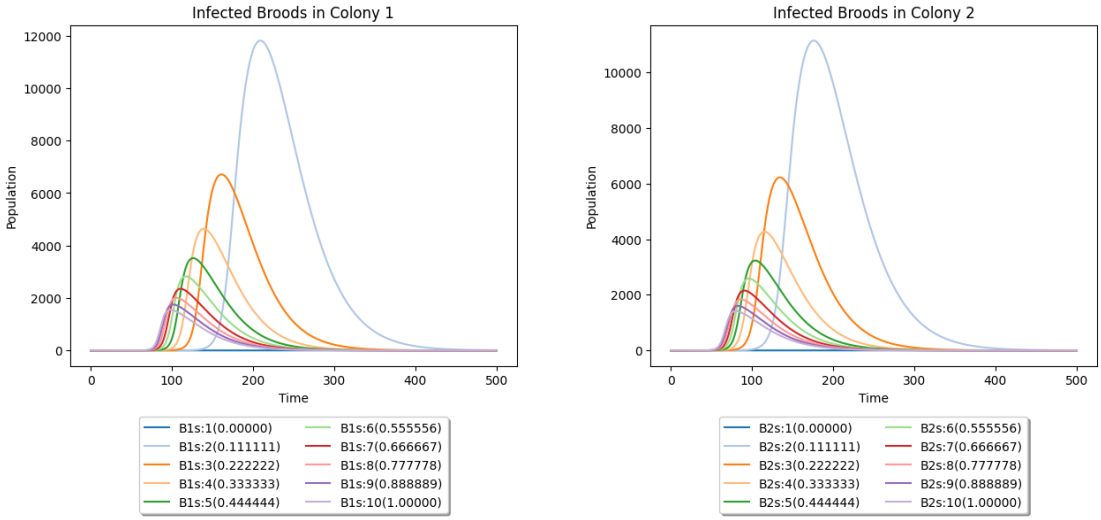

Figure 18. Effect of varying φ_1 on brood dynamics with infected adult in Colony 2.

The observed graphs indicate that as the parameter φ_1 decreases, the onset of the first brood infection decelerates, albeit with a higher peak population. Consequently, we conducted experiments with smaller values of this parameter and investigated their impact on the dynamics of adult honeybees. The findings are presented below.

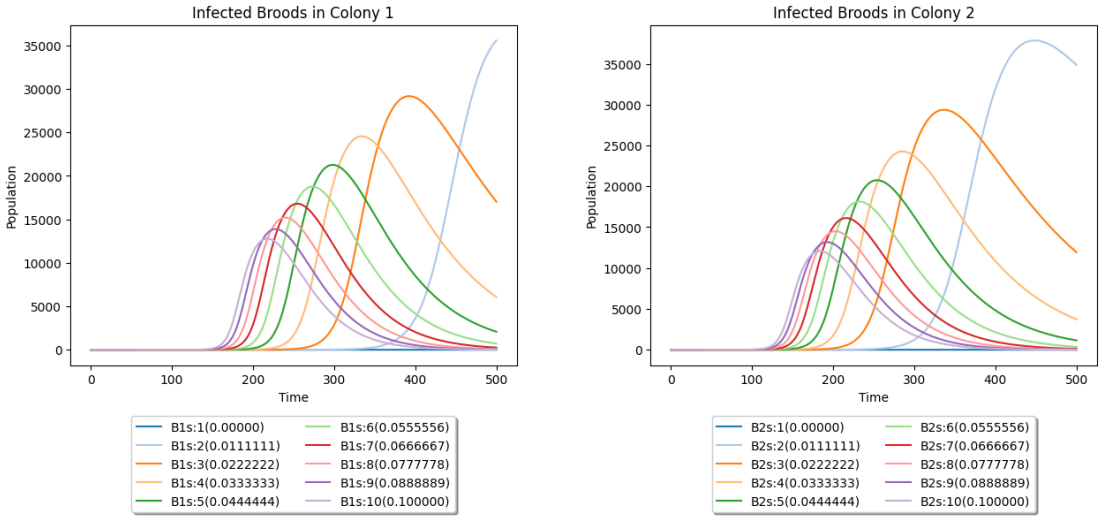

Figure 19. Effect of varying φ_1 [0, 0.1] on brood dynamics with infected adult in Colony 2.

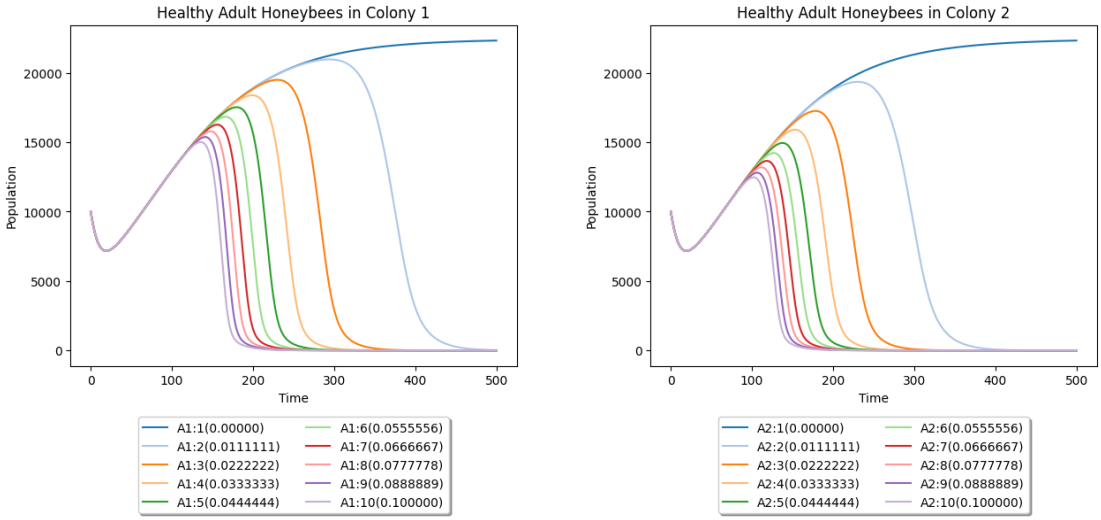

Figure 20. Effects of varying φ_1 [0, 0.1] on adult honeybee dynamics with infected adult in Colony 2.

Further observations reveal that smaller values of φ_1 lead to delayed onset of AFB infection; however, if left unaddressed, they result in more severe consequences in colony health.

Now, we proceeded to another important parameter, σ, which is the percentage of clean cell combs that will be contaminated by AFB spores (Error! Reference source not found.). The following results can be seen in the figures below.

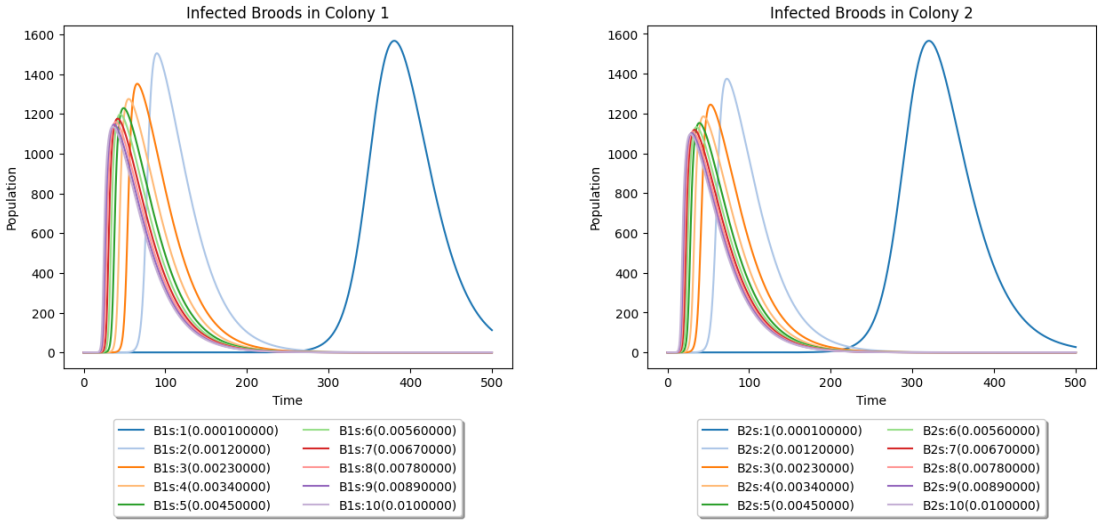

Figure 21. Effect of varying σ on brood dynamics with infected adult in Colony 2.

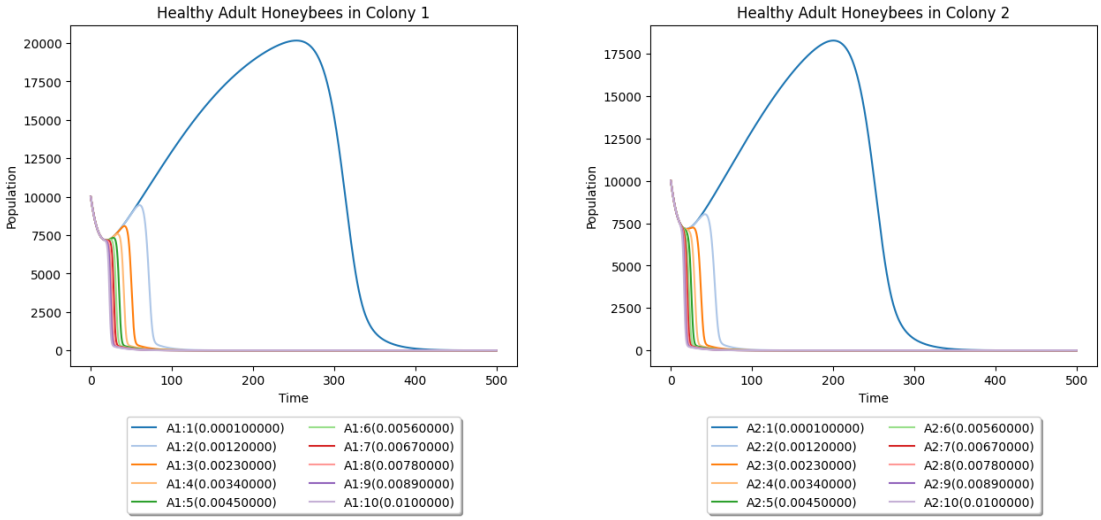

Figure 22. Effects of varying σ on adult honeybee dynamics with infected adult in Colony 2.

These results indicate that smaller values of σ also slow down the spread of infection within the colony. This suggests that apiary farmers may have more time to address the spread of AFB within their apiaries.

Based on these findings, we further explored the effects of different combinations of two parameters on brood infection onset using heat maps. Specifically, we varied both d_2 and γ_2, and the resulting heat map is depicted below.

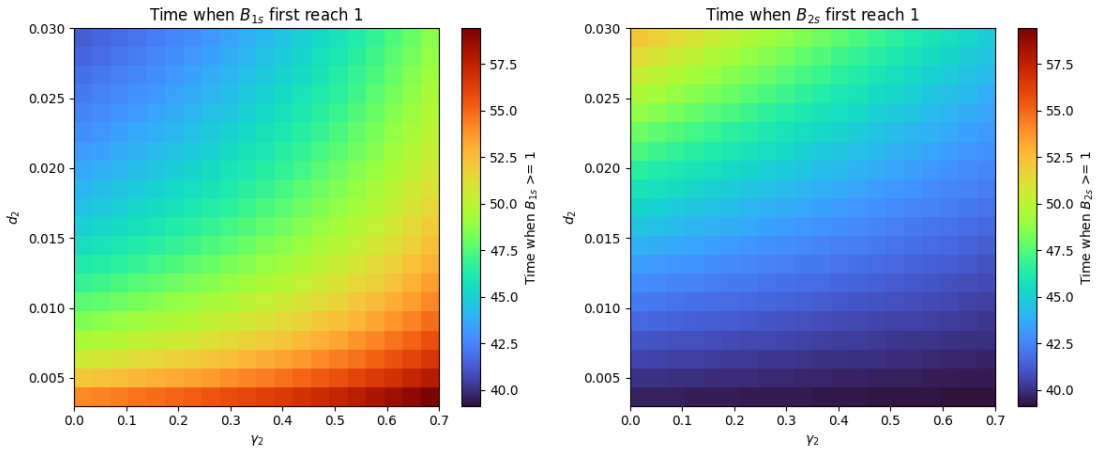

Figure 23. Effects of varying d_2 and γ_2 on brood dynamics with infected adult in Colony 2.

Analyzing the heatmaps, we determined the relationship between different parameter combinations and the onset of the first brood infection in days. Notably, when d_2 is low and γ_2 is high, the onset of brood infection occurs slower in Colony 1 but faster in Colony 2. This suggests that limited drifting in Colony 2

facilitates faster infection spread within their colony. Consequently, rejected adult drifters from Colony 2 have a higher likelihood of getting lost to another colony or returning to their own, accelerating the onset of infection.

Furthermore, we investigated the combined effects of two important parameters, σ and φ_1, on the onset of brood infection. The results are displayed in the heatmaps below.

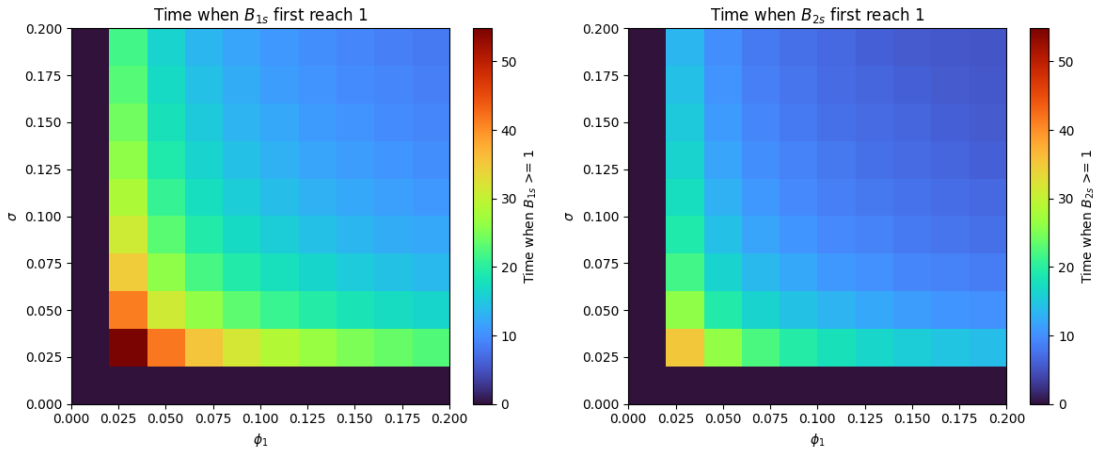

Figure 24. Effects of varying σ and φ_1 on brood dynamics with infected adult in Colony 2.

The heatmaps above illustrate that lower values of both parameters lead to a slower onset of the first brood infection. This observation underscores the significant influence of these parameters on the timing and severity of AFB outbreaks, highlighting their importance in formulating effective disease control strategies for beekeeping practices.

Finally, the last simulation was the effect of varying the parameters, σ and α_2. The importance of this relationship lies in how environmental contamination influences the likelihood and rate of infection transmission within the colony. A higher σ value means that more clean cell combs are contaminated, which in turn increases the exposure of adult bees to AFB spores and thus increases the likelihood of infection transmission, as captured by α_2. The heatmap is shown below.

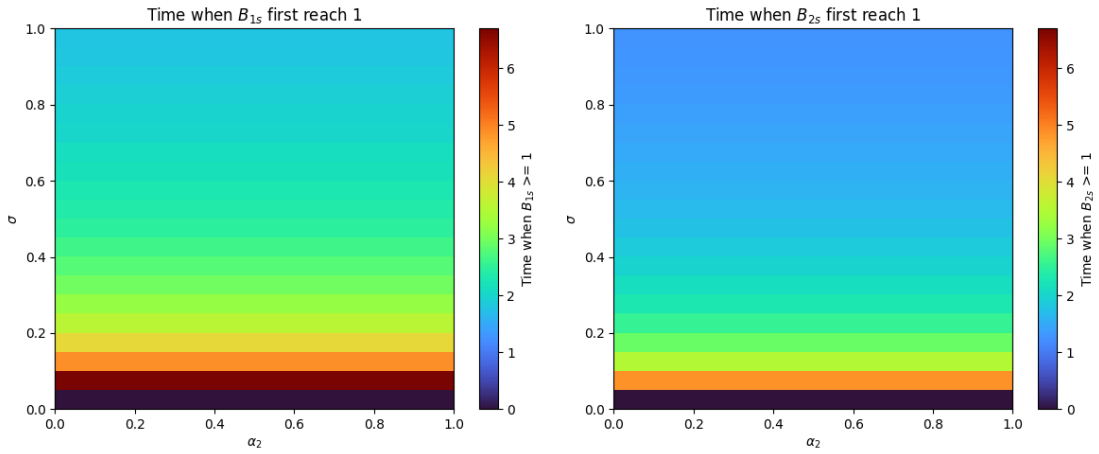

Figure 25. Effects of varying σ and α_2 on brood dynamics with infected adult in Colony 2.

From the heatmap above, we can see that α_2 does not really affect the first infection on broods. It is more important to look at σ, which denotes the percentage of clean cell combs contaminated by AFB spores, is particularly significant for assessing the vulnerability of honeybee colonies to AFB infection. A higher value of sigma indicates a greater likelihood of AFB contamination in the colony's brood cells, leading to more rapid and extensive spread of the disease.

The obtained results are further elaborated upon in the Discussion section of the paper.