Understanding Flight Patters of Parasitoid Wasps

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Abstract

Parasitoid wasps play a vital role in agriculture as a biological form of pest control, however their patterns of movement are poorly understood. Recent research has shown that while parasitoid wasp movement largely is a result of the local wind patterns, there is the potential for wasps to travel upwind even in unfavorable conditions. Using IB2d to simulate fluid flow around objects in 2D and Planktos to incorporate flow data with an agent-based model, this paper attempts to better understand how parasitoid wasps may attempt to fly upwind. The results suggest that factors such as flight velocity, wind velocity, wasp endurance, and trap size all play a role in determining whether a wasp has the ability to reach a desired location upwind. Further analysis using Finite Time Lyapunov Exponent (FTLE) methods suggests that the distance from which a wasp may be able to detect a trap, which is limited by the biology of wasp eyes, is the biggest determinant in whether a wasp will successfully reach the trap or ultimately be advected away by the wind. Future studies may want to consider wasp flight in 3D or more complex wasp flight patterns.

1 Introduction

Agricultural pests cause billions of dollars worth of damage yearly, and are known to affect food insecurity rates in developing countries that lack access to high-tech industrial farming equipment [1, 2]. These pests are frequently combated with chemical pesticides, however, this method can be costly and is known to cause extensive damage to the local environment. A less common method of pest control is through more natural means. Biological pest control involves the use of parasitoid wasps which naturally consume the eggs, larvae, and sometimes pupae of many agricultural pests. These parasitoid wasps, of the order *Hymenoptera*, are a group of wasps often less than 1mm known to parasitize many pests including aphids, caterpillars, and worms. As such, some farmers may choose to release these parasitoids in a crop field in order to control pest populations through less harmful biological means.

Unfortunately the process is not as simple as just releasing the parasitoids in the middle of a field with crops. Due to the small size of these wasps, they struggle to fly quickly or for long periods of time, and so the distribution is generally a function of the wind patterns at the time of release. Experimental data has found wasps upwind of their release point, but the mechanisms of upwind flight are poorly understood [3]. Some experiments such as [4] have attempted to study the movement of wasps upwind in a wind tunnel giving a controlled environment, however *in situ* experiments are limited.

Figure 1: An aphid parasitoid wasp. Photo: John Davidson, University of Maryland [5].

This study aims to examine possible mechanisms of flight by wasps in unfavorable conditions by replicating the results in [4], and find the factors that play significant roles in flight. IB2d will be used to generate 2D flow fields around an obstacle. Using an agent-based model to simulate wasp flight behavior, the wasps will attempt to navigate in a complex flowing environment and their behavior will be examined. In the future these results may be generalized and applied to larger simulations that consider large parasitoid populations as well as extensive consideration of the structure of crop fields.

2 Methods

Sarig et al. ([4]) experimentally found that when placed in a wind tunnel with a trap of varying sizes upwind, there was a linear correlation between the flight velocities of the wasps and the number of wasps which successfully reached the traps. The wind velocity in the tunnel was also found to have a linear correlation with success rate. A simple model to describe the wasp movement replicated these findings, however the data gathered with this model was limited. The wasps were given a set of rules for flight: when within a defined range to detect the trap, wasps would fly directly toward the trap with the option of compensating for wind advection. If the wasps did not detect the trap, they would undergo a simple random walk at a fraction of their maximum flight speed.

To expand on these findings, a new model was built that would replicate these results as well as gather new data. To replicate the experiment in [4], IB2d was used to calculate the flow field of wind moving past a circular obstacle. Then Planktos was used to integrate IB2d data as well as build the agent-based model for describing parasitoid wasp flight.

2.1 IB2d

There was an initial attempt to reproduce the results found in [4] using computational methods. Due to the availability and ease of use of the immersed-boundary method for solving complex fluid structure interactions (FSIs), IB2d was chosen as a suitable program for solving the system [6, 7, 8]. Simulations were run of a 1.0m$\times$0.2m domain, with a cylinder (a circle in this two dimensional case) of varying radius centered at $(0.25, 0.1)$. There was a forcing function giving the desired velocity of the system from 0.0m - 0.10m with flow in the positive x direction. This location was chosen to give the flow enough distance to stabilize before interacting with the cylinder, and the cylinder was located far enough upstream for the flow behavior to develop on the leeward side of the structure. Fluid velocity was varied with the following values: 0.0m/s, 0.12m/s, 0.16m/s, 0.22m/s, 0.29m/s, 0.35m/s, 0.51m/s. The cylinder radius was varied with the following values: 0.005m, 0.01m, 0.02m, 0.04m. Combining these two variables gave 28 different combinations.

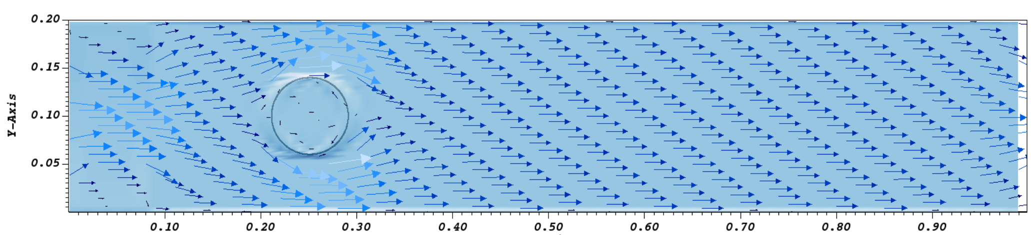


Figure 2: An example setup in IB2d of a single cylinder in a domain. Parameters are $r = 0.04$m, $v_f = 0.29$m/s.

In IB2d, the resolution was set to a 100$\times$100 Eulerian grid, with a time-step of 1.0e-5 and a print_dump value of 400. This gives $dt = 400 \cdot 1.0\text{e}{-5} = 0.004$s. The total simulation time was 1.0s. Since the goal of this experiment was to examine flight of insects through air, standard values of density and dynamic viscosity were selected: $\rho = 1.204$ kg/m^2, $\mu = 1.813\text{e}{-5}$ N$\cdot$s/m^2.

2.2 Planktos

Planktos is an agent-based modeling framework that considers the movement of agents in a fluid which are assumed to be small enough that their effect on the surrounding flow is negligible [9]. These agents can be small particles or organisms such as plankton in the ocean or parasitoid wasps flying through the air. Due to its availability as an open source software package, ability to easily incorporate VTK data from IB2d, and ease of use, Planktos was chosen as the agent-based modeling framework for studying parasitoid wasp flight.

With some modification, the rules for agent behavior were taken from [4]. In most cases, the wasps were initialized randomly in a circular region centered at $(0.4, 0.1)$ with radius 0.04m. In the remaining cases, as will be noted, the wasps were initialized randomly throughout the entire domain, which was done to understand the general patterns of movement. Wasps were considered to move at the local fluid velocity with an initial active flight velocity. When initialized, the wasps would undergo a simple random walk at a scalar factor f_c of their maximum flight velocity v_w ($f_c = 0.7$). This would continue until the wasps had identified the target or were advected out of the simulated domain. When the wasps are within the necessary distance to recognize the targets, they would be considered "locked in" and would fly toward the center of the target at the maximum flight velocity v_w for the defined endurance time T_e. Detection distance for the trap was found to be related to trap size in [4] due the biology of wasp eyes. At any point during this period if a wasp reached the trap, which was recognized as an immersed boundary collision in Planktos, it was be considered "stuck" and all further movement ceased. After the defined endurance time T_e has elapsed, which began once the wasp was "locked in", the wasp was be considered exhausted. At this point, the wasp would fly at a scalar factor f_e of the maximum flight velocity v_w ($f_e = 0.1$), and would still attempt to reach the trap if within range. Otherwise, the exhausted wasp would revert to a simple random walk.

Table 1: Value and description for each parameter used.

Parameter	Description	Value
v_w	Maximum flight velocity (m/s)	0.35, 0.42, 0.51
v_f	Ambient fluid velocity (m/s)	0.0, 0.12, 0.16, 0.22, 0.29, 0.35, 0.51
T_e	Endurance time (s)	0.6, 1.0, 3.0
f_e	Exhausted speed factor	0.1
f_c	Random walk speed factor	0.7
r	Trap radius (m)	0.005, 0.01, 0.02, 0.04
dt	Time step (s)	0.005

In order to calculate movement for each time step, which would vary, a series of steps were taken. First, the vector from each agent to the center of the trap was found, now known as $\boldsymbol{v}$. The detection distance of the trap from the center is calculated as $d = 3.35 \cdot 2r + r = 7.7r$, where r is the radius of the target and the second r term is added to allow the detection distance to begin at the edge of the trap. If $\|\boldsymbol{v}\| <= d$, then it was assumed the wasp has detected the trap and was considered "locked in".

There are a number of optional characteristics that were given to the wasps. The first being a delay in the rate at which individual wasps could update their direction. This delay was customizable, and occurred after a desired number of time steps. This delay was assumed to be due to the rate at which a wasp can flap its wings, and was assumed to be 5 time steps. When the wasp was unable to update its direction, it continued flying with its previous velocity. The next customizable trait was the ability to add variance in the direction of travel. Wasp flight was assumed to be imperfect, and other variables that could not be accounted for were included in this variance. Therefore, with the new velocity vector $\boldsymbol{v}$, the direction was varied on a normal distribution with standard deviation $\sigma = \pi/6$.

After the velocity vector had been determined, whether it was being updated or continued from previous time steps, it was then normalized. Following the normalization, the wasp was checked to be exhausted. If the wasps had not recognized the target, were assigned random walk paths for $\boldsymbol{v}$.

Finally, the flight vector was determined for each wasp giving

$$\boldsymbol{v}_{flight} = \begin{cases} v_w f_e \boldsymbol{v}, & \text{if exhausted} \\ v_w f_c \boldsymbol{v}, & \text{if not locked on the trap} \\ v_w \boldsymbol{v}, & \text{if not exhausted and locked on the trap} \end{cases}$$

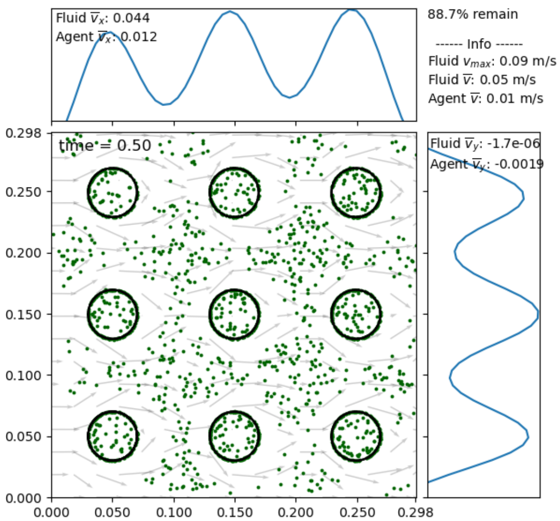
If any wasp was determined to have collided with an immersed boundary (the target circle), then it was considered "stuck" and would not be moved for the remainder of the simulation.

Simulations were run in Planktos across all parameters mentioned above with an initial swarm size of 2500 agents, $dt = 0.005$, and 150 time steps run giving a simulation time of 0.75s. The variables tracked were mean arrival time, the total number of wasps that had successfully reached the trap, and arrival location on the trap. In each parameter case, the number of wasps that reached the trap was averaged across three trials. When examining mean arrival time and arrival distribution, a single trial was run. Linear regression was then performed to determine correlation between success rate or mean arrival time and the varied parameters.

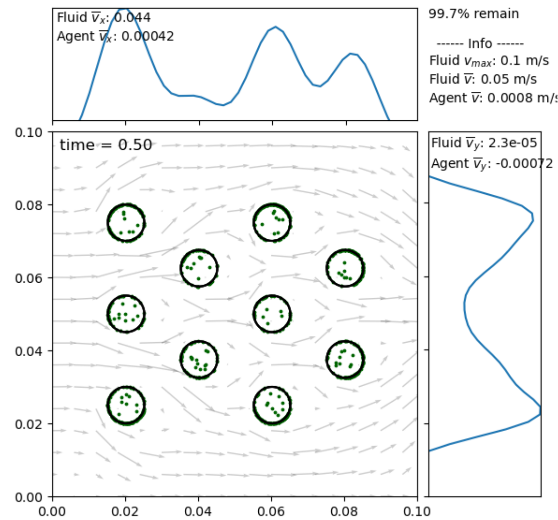
2.3 FTLE

After the statistical analysis was done, Finite Time Lyapunov Exponent (FTLE) fields were calculated and plotted to determine if there was any emergent behavior exhibited by the wasps that could not be found through simple linear regression. Along with the case where air flowed around a single cylinder, tests were done with multiple cylinders including a 3×3 grid arrangement and a 3-2-3-2 staggered arrangement that was horizontally symmetrical. Both arrangements are shown in Figure 3. When placed in an environment with multiple traps, the wasps were programmed to fly to the nearest trap recognized.

When calculating FTLE, any stochastic processes would have obscured the results and made Lagrangian Coherent Structures (LCS) more difficult to visualize, as can be seen compared in Figure 4. For this reason all random processes that were included in earlier analyses were disabled during FTLE calculations.

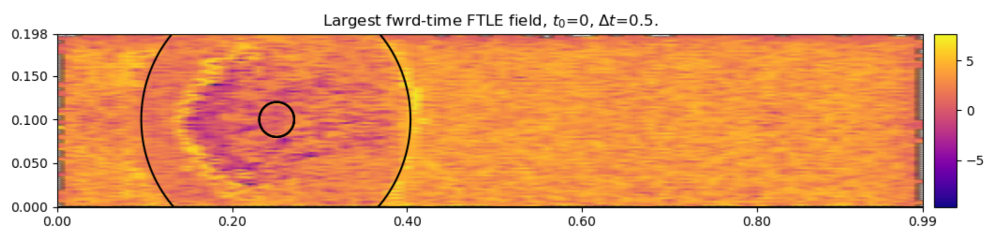


(a) A 3×3 grid of traps.

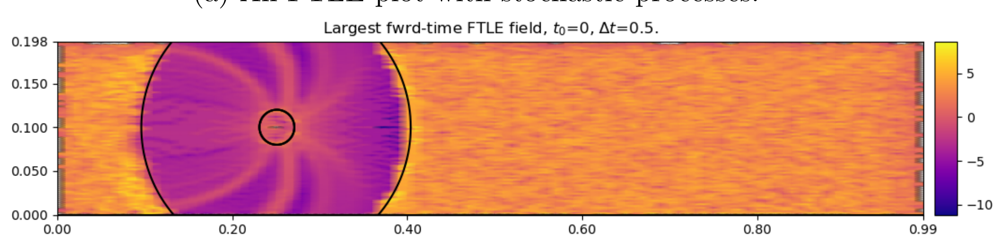


(b) A staggered grid of traps in a 3-2-3-2 arrangement.

Figure 3: An example setup for multiple traps in the same domain. Green dots represent wasps in motion. Parameters are $r = 0.005$m, $v_f = 0.12$m/s.



(a) An FTLE plot with stochastic processes.



(b) An FTLE plot without stochastic processes.

Figure 4: The loss of information with stochastic processes is the reason that FTLE calculations were performed on deterministic systems.

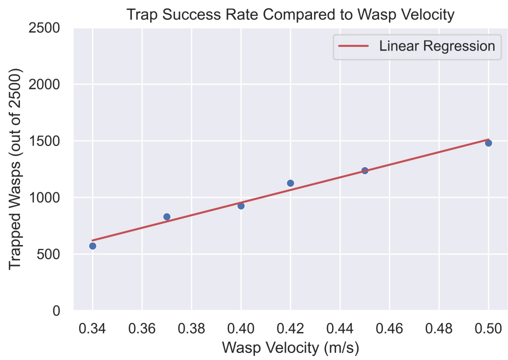
3 Results

3.1 Success Rate

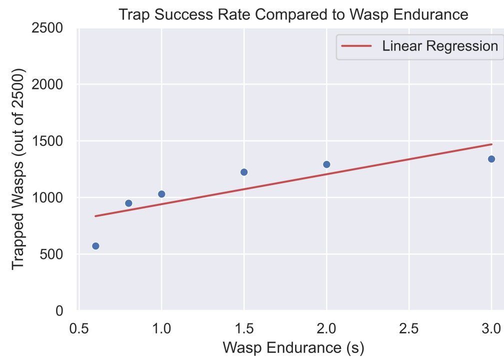
Figure 5a shows the relationship between wasp flight velocity and the number of trapped wasps. After varying the maximum wasp velocity v_w while holding other variables constant

($r = 0.02$m, $T_e = 0.6$s, $v_f = 0.51$m/s), linear regression was performed and a strong correlation was found between the number of wasps which reached the trap and an increased flight speed ($r^2 = 0.9818$).

Figure 5b shows the relationship between wasp endurance and the number of trapped wasps, with $r = 0.02$m, $v_w = 0.34$m/s, and $v_f = 0.51$m/s. From this, linear regression showed a weaker positive correlation between endurance time and the number of wasps which reached the trap ($r^2 = 0.6882$). It is possible that if lower endurance times were simulated this trend may be logarithmic.



(a) The relationship between w_v and success rate.



(b) The relationship between T_e and success rate.

Figure 5: Figure 5a shows the relationship between w_v and success rate with $r = 0.02$m, $T_e = 0.6$s, $v_f = 0.51$m/s. Figure 5b shows the relationship between T_e and success rate with $r = 0.02$m, $v_w = 0.34$m/s, and $v_f = 0.51$m/s.

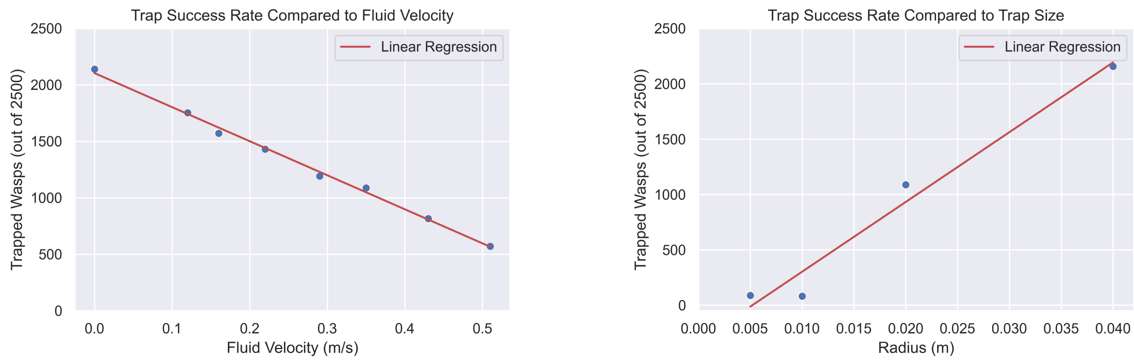
Next in Figure 6a the surrounding fluid velocity was altered with $r = 0.02$m, $v_w = 0.34$m/s, $T_e = 0.6$s and the number of trapped wasps was mapped. Linear regression showed a very strong negative correlation between these variables, and an increase in fluid velocity significantly reduced the number of wasps which successfully reached the trap as seen in 6a ($r^2 = 0.9961$).

As shown in Figure 6b, issues arose when attempting to vary the radius and holding other variables fixed ($v_w = 0.34$m/s, $T_e = 0.6$s, $v_f = 0.51$m/s) which will be discussed later and will need to be recognized before the results should be interpreted, however the data that was gathered shows a strong positive linear correlation between the number of wasps which successfully reached the trap and an increased trap size ($r^2 = 0.9713$).

3.2 Mean Arrival Time

Again when testing for mean arrival time, a strong correlation was found between an increasing fluid velocity and a later arrival time for the wasps ($r^2 = 0.9350$). This was done with $v_w = 0.34$m/s, $T_e = 0.6$s, $r = 0.02m$ held fixed.

The wasp success rate and mean arrival time in cases with multiple traps in staggered or grid arrangements were not examined.



(a) Comparing v_f with the number of wasps that successfully reached the trap showed a strong negative correlation.

(b) Increasing r showed a positive correlation with success rate, however there were problems which are addressed in Section 4.4.

Figure 6: Figure 6a shows the relationship between w_v and success rate with $r = 0.02$m, $T_e = 0.6$s, $v_w = 0.34$m/s. Figure 6b shows the relationship between r and success rate with $T_e = 0.6$s, $v_w = 0.34$m/s, and $v_f = 0.51$m/s.

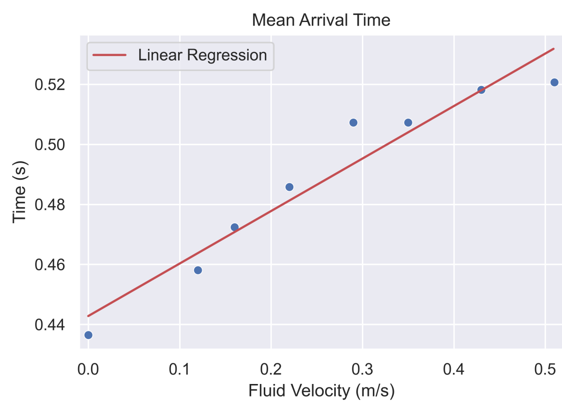
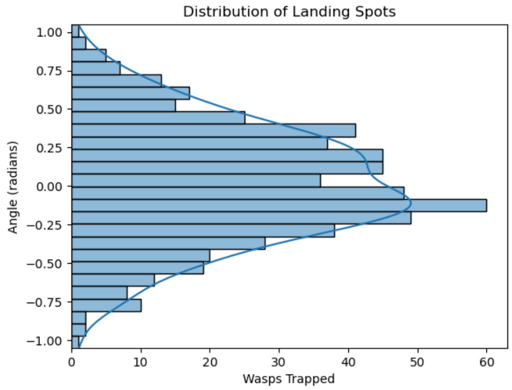


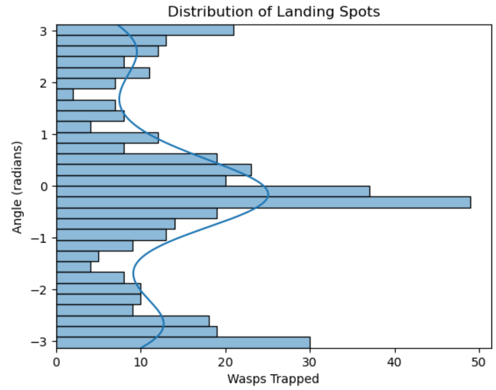
Figure 7: The mean arrival time for wasps that reached the target given $v_w = 0.34$m/s, $T_e = 0.6$s, $r = 0.02$m was positively correlated with increasing v_f.

3.3 Arrival Location

The landing spot on the trap by a wasp was found by calculating the angle from the center of the circle relative to a vector in the direction of flow. The resulting angle in radians was mapped. In the case where wasps were initialized in a defined circular region downwind of the trap (Figure 8a), the distribution was found to be approximately normal with most wasps landing on the leeward side of the trap where there appeared to be a region of low fluid velocity. Meanwhile when the wasps were initialized randomly within the domain (Figure 8b), the distribution of arrival locations again showed an increased amount of wasps landing on the leeward side of the trap however there was also a significant, albeit lower, amount of wasps that landed on the windward side. Both tests did imply that relatively few wasps are likely to land on the sides of the trap where fluid is moving tangential to the trap surface.



(a) Distribution of arrival locations given an initialization downwind of the trap.



(b) Distribution of arrival locations given random initialization.

Figure 8: Distribution of landing spots on the trap in radians with 0 radians being directly downwind. Parameters are $r = 0.02$m, $v_w = 0.51$m/s, $T_e = 0.6$s.

3.4 FTLE

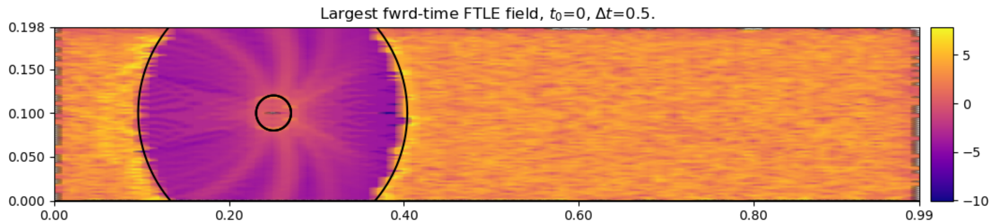
Calculating the FTLE values for different fluid velocities gave results that showed a progression to more defined features as shown in Figure 9. The outer black circle represents the detection distance for wasps with respect to the trap, which is the inner black circle. The bright orange lines within the detection distance represent separatrices, with different movement patterns on either side of these lines. There are approximately six different separatrix lines that develop more clarity as the fluid velocity increases. In Figure 9a, the separatrix lines are very faint and lack a defined structure, however in Figures 9b and 9c, there is a clear pattern of wasp movement.

FTLE fields for the tests with multiple traps did not yield any emergent behavior, which can be seen in Figure 10. The case with a simple 3×3 grid (Figure 10a) showed movement toward the nearest cylinder with the effect of the surrounding fluid flow being negligible. There was some behavior shown in the staggered case (Figure 10b) where separatrix lines visibly divided wasps based on their trap choice, however patterns similar to cases with one trap did not appear.

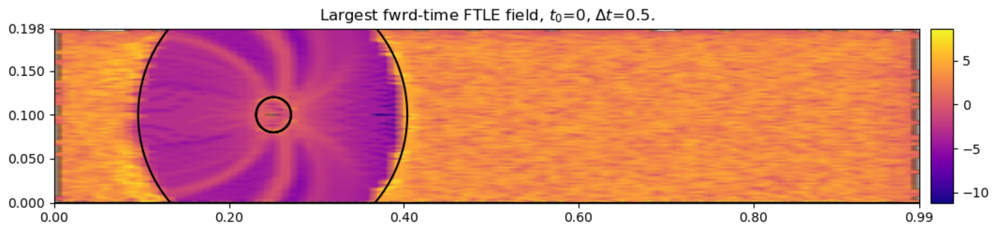
4 Discussion

4.1 Success Rate

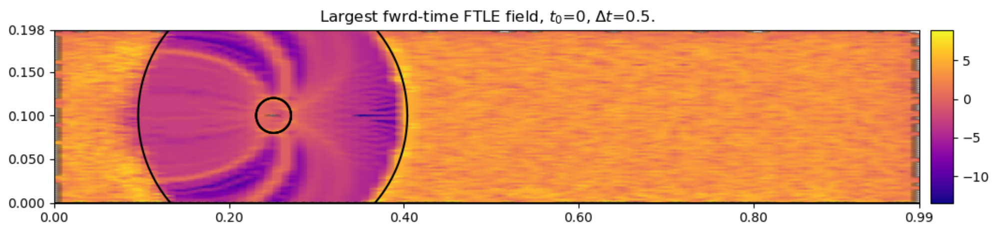
The initial goal of this investigation was to replicate the results found in [4] and test the Planktos framework, which was successfully done. The number of wasps that successfully reached the trap grew linearly with increased flight velocity and increased endurance as well as decreased linearly with increasing fluid velocity. This was all expected and the results show strong correlation even with stochastic processes built in to the model. Strong correlation validates the model and suggests that Planktos can successfully replicate experimental data.



(a) FTLE with $v_f = 0.12$.



(b) FTLE with $v_f = 0.35$.

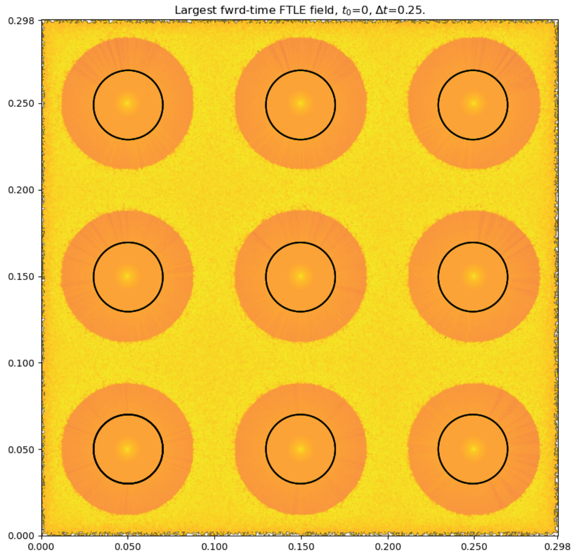


(c) FTLE with $v_f = 0.51$

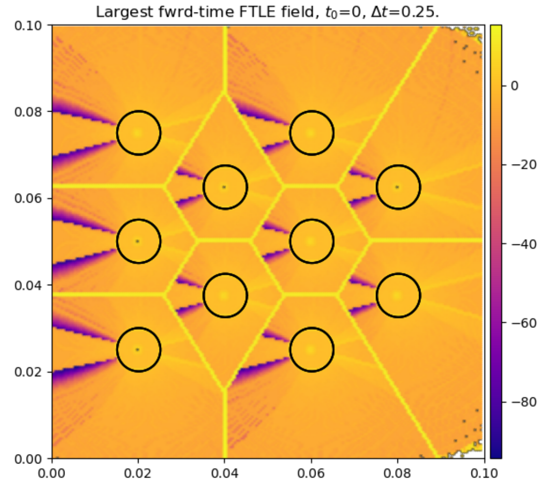
Figure 9: FTLE field of the swarm experiment with $v_w = 0.34$m/s, $T_e = 0.6$s, $r = 0.02$m. The outer black circle indicates detection distance for the wasps.

We have also found that the ability for wasps to fly upwind depends largely on the ambient fluid velocity (shown in Figure 6a) and biological factors including flight speed and endurance time (Figure 5a and Figure 5b). Given that average wind speeds in fields are typically higher than the velocities tested here, the results suggest that parasitoid wasps must wait until conditions are favorable for flight if there is any attempt to fly upwind toward more desirable areas.

Initial analysis of the wasp success rate when compared to trap size suggested a linear relationship as well, however only four values were gathered and so more investigation is needed to determine the true relationship. However, issues arise when attempting to compare the varying trap sizes. Detection distance for the wasps depends on the trap size, and the wasps were initialized in a region downwind approximately 0.15m from the center of the trap in every trial. This resulted in most of the wasps being initialized within the detection distance for traps with radius 0.02m and 0.04m, however very few wasps would detect the trap with radius 0.005m. Using a random initialization to gather the data instead would create a similar issue, as fewer wasps would be initialized within the detection distance of the smaller traps skewing the results. Due to this problem, it is difficult to obtain any meaningful results when comparing the different trap sizes.



(a) FTLE plot of the 3×3 grid of tiled traps.



(b) FTLE plot of the staggered trap grid.

Figure 10: Figure 10a shows simple behavior from the wasps, however in Figure 10b there are separatrix lines that determine wasp movement. Parameters are $v_w = 0.34$m/s, $T_e = 0.6$s, $v_f = 0.12$m/s, $r = 0.005$m.

4.2 Mean Arrival Time

The mean arrival time of the wasps gave interesting results as well. The relationship between increasing fluid velocity and increasing mean arrival time is appears linear (in Figure 6b). It is possible that the trend is logistic, as after some fluid velocity it becomes impossible for the wasps to reach the trap and the trend plateaus. Some variation does appear in the data and it would be useful to gather more data with higher velocities to determine whether the trend is truly linear or logistic.

4.3 Arrival Location

Comparing the distribution of arrival locations on the trap was another method of validating the results found in [4]. When wasps were initialized directly downstream, the distribution was approximately normal (Figure 8) with the majority of the wasps landing on the leeward side of the trap. Very few, if any, landed on the windward side of the trap, which was expected as it was unlikely for a wasp to travel around the trap without eventually interacting with the immersed boundary, and these results were expected.

On the other hand, the random initialization case had not been tested before and the results showed a distribution that was not expected. Rather than the simple expectation where there is a uniform distribution of wasps across the entire trap, there appeared to be more wasps arriving on the side of the trap directly upwind as well as the leeward side similar to the defined initialization case mentioned above. Very few wasps would reach the trap on the sides where wind shear was highest with respect to the surface of the trap, and these wasps were instead more likely to collide with an immersed boundary on the leeward side.

4.4 FTLE

These results are corroborated by the FTLE analysis. While it is more difficult to see in cases with lower fluid velocity, Figure 9c shows clear trends with specific regions trending toward the trap. There are only a few regions that trend toward the sides of the trap not in the direction of the wind, and these regions appear to be small compared to areas upwind or downwind that contain most of the wasp arrivals.

FTLE analysis of each fluid velocity suggests that the primary factor that determines whether a wasp might reach the trap is the detection distance. The outer black circle on the FTLE plots in Figure 9 shows the detection distance for each trap and shows a clear boundary between wasps that were able to reach the trap and those that never did. Therefore while factors such as fluid velocity, flight velocity, and endurance may affect success rate, it appears that the detection distance is the primary determinant of wasp flight patterns.

While it was expected that detection of the trap would play a significant role in the number of wasps reaching the trap, it was thought that other variables would be just as important. However this FTLE data suggests that there exists a clear difference between wasps that detect the trap and those that are initialized out of the detection range. The clear boundaries at the detection lines show that factors such as flight velocity and endurance are secondary to trap recognition.

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