Foraging Fruit Flies: Lagrangian and Eulerian Descriptions of Insect Swarming

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Abstract

In this work, I seek to model swarms of fruit flies, *Drosophila melanogaster*, whose flights are characterized by straight flight segments interrupted by rapid turns called saccades. These flights are reminiscent of Levy-distributed random walks which are known to lead to efficient search behavior. I build two types of model for swarms of foraging fruit flies, whose behavior depends on swarm density and chemoattractant concentration, using rules inspired by experimentally observed flight patterns. First I will present a Lagrangian model where the path of each individual fly is tracked. I will also consider an Eulerian model where the fruit fly density evolves as a function of time and position in space. I will discuss the advantages and disadvantages of the two models and the relationship between them.
Contents

Abstract iii

Acknowledgments ix

1 Introduction 1

1.1 Swarm Modeling 2

2 Biological Background 5

2.1 Collective Action 5

2.2 Free Flight 7

3 Lévy Flights and Searches 11

3.1 The Lévy Flight 11

3.2 Lévy Searches 12

4 Lagrangian to Eulerian Formulations 17

4.1 A Simple Case 17

4.2 Extension to Density-Dependent Behaviors 19

5 A New Direction 21

5.1 Pursuit of a 1-D Lagrangian Model 21

5.2 Search Efficiencies of the 1-D Schemes 30

5.3 The One Dimensional Eulerian Framework 34

5.4 Lagrangian Modeling in Two Dimensions 38

6 Conclusions 41

Bibliography 43
## List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Diagram of Two-phase Foraging</td>
<td>6</td>
</tr>
<tr>
<td>2.2</td>
<td>A Characteristic Flight Path for a Fruit Fly</td>
<td>8</td>
</tr>
<tr>
<td>2.3</td>
<td>A Flight Path with an Odor Source</td>
<td>9</td>
</tr>
<tr>
<td>3.1</td>
<td>A Lévy Flight in Two Dimensions</td>
<td>13</td>
</tr>
<tr>
<td>5.1</td>
<td>Moments for 1-D Model</td>
<td>23</td>
</tr>
<tr>
<td>5.2</td>
<td>Position Histograms for 1-D Swarm</td>
<td>24</td>
</tr>
<tr>
<td>5.3</td>
<td>Moments for Foraging Model</td>
<td>25</td>
</tr>
<tr>
<td>5.4</td>
<td>Position Histograms for Foraging Model</td>
<td>26</td>
</tr>
<tr>
<td>5.5</td>
<td>Swarm Moments for Interacting Model</td>
<td>29</td>
</tr>
<tr>
<td>5.6</td>
<td>End of Simulation Positions</td>
<td>30</td>
</tr>
<tr>
<td>5.7</td>
<td>Position Histograms for Interaction</td>
<td>31</td>
</tr>
<tr>
<td>5.8</td>
<td>Search Efficiencies I</td>
<td>32</td>
</tr>
<tr>
<td>5.9</td>
<td>Search Efficiencies II</td>
<td>33</td>
</tr>
<tr>
<td>5.10</td>
<td>Fluxes into and out of a Rectangle</td>
<td>35</td>
</tr>
<tr>
<td>5.11</td>
<td>The 2-D Flight Path of a Foraging Fly</td>
<td>39</td>
</tr>
<tr>
<td>5.12</td>
<td>A Radial Histogram of Position</td>
<td>40</td>
</tr>
</tbody>
</table>
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Chapter 1

Introduction

The aggregation of fruit flies, *Drosophila melanogaster*, about a source of food is an everyday, albeit undesirable, phenomena. Biologically, fruit flies gather in groups to engage in a host of social behaviors. One of these is foraging for food sources in areas where food is not readily available to each individual, but rather must be found by the group. The idea that the group can search for food more effectively than the individuals can is fairly simple to grasp, but the behavior that has been observed leads to interesting mathematical questions.

In the swarm, an individual’s flight path is characterized by straight jaunts followed by quick and random changes in direction, known as saccades. The flight path of a fruit fly is essentially a random walk in the two horizontal directions, with vertical behavior much less interesting. When a fly forages, the length of the straight jaunts is controlled by the concentration of scent (chemoattractant) that the fly experiences (see Frye and Dickinson (2004)). Experiments indicate that the fly has no memory with regard to scent and cannot voluntarily move up a chemoattractant gradient, by biasing its saccade direction. In addition, *Drosophila* swarms are observed to act cooperatively in two distinct modes (see Tinette et al. (2004)). Certain flies in the group will travel away from the greater swarm, searching for and evaluating potential food sources, while the others stay in the group and follow the successful searchers. Interestingly, flies that participate in searching are biologically no different than the grouped flies and a single fly’s mode of behavior will vary with time. With these factors in mind, a fruit fly swarm poses several questions:

1. If an actor is searching, how can it locate the source of an attractant without being able to consciously move toward the source?
2. How do actors, with fly-like behavior, perform searches most efficiently and how does that relate to the observed biology?

3. How is it that biologically identical flies can demonstrate two modes of behavior, presumably based on an individual’s preference, such that a swarm cooperates in foraging as opposed to competing or acting individualistically?

These are the motivating questions that I have chosen to guide the work in this thesis. They turn out to be very rich mathematically, requiring concepts from several fields to be used to model, analytically and computationally, a typical fruit fly swarm. Many of the techniques I will share in the following pages come from previous studies of insect or animal aggregation which I will heuristically describe before delving into fruit fly behavior.

1.1 Swarm Modeling

Aggregation and collective movement abound in nature. A flock of birds headed South in November, a school of fish in the ocean, and a swarm of insects crowded onto a piece of fruit are all examples of aggregation and grouping behavior. The reasons for aggregation are many: protection from predators or the environment, mating, traveling, and foraging are all reasons for animals to form into groups and perform some collective action or simply interact socially amongst themselves. The kinds of behaviors that a swarm can exhibit can be as diverse as the organisms that form them. The structure, movement and lifetime of a swarm can vary because of the local environment, the constituent organisms, or the reasons for the social interaction. How these larger behaviors come from a set of organisms is an interesting question that has long been considered by biologists but has, in the last half century, peaked the interest of mathematicians. The mathematics of swarms can pose hard problems, with non-linearity and large parameter spaces, but swarming does lead to interesting findings regarding how local dynamics can affect global structure and how biological systems can display essentially optimized behavior.

Swarms have been considered from a modeling perspective in two primary fashions. Lagrangian swarming models describe a swarm at the level of the individual, where an individuals’ behavior is based on the local environment, and then conclusions can be drawn about the swarm through numerical simulations or estimates on the structure of the swarm after long times. The work by [Mogilner et al., 2003] is an example of this approach.
They investigate the social forcings commonly used to model swarms and look for conditions on swarm stability. The other tool used to describe swarms is known as the Eulerian framework. Swarms, in Eulerian models, are thought of in a continuum sense - where equations similar to those found in fluid mechanics describe some attribute of the swarm, typically the density of individuals. These governing equations, are typically nonlinear partial differential equations and hence must be solved numerically. Topaz and Bertozzi (2004) provide an excellent example of this approach. Some studies start with a Lagrangian framework and then use it to build an Eulerian model using limiting cases and simplify assumptions. This is an interesting approach and one which I would like to use in my work on fruit flies.

The behavior that I will seek to model for *Drosophila* is similar to the behavior exhibited by the bacteria, *Escherichia coli*, which is highly studied. Like the flies’ jaunts and saccades, bacteria’s trajectories are characterized by runs and tumbles. A run is a path swam in a straight line and a tumble is a random change in direction. Berg (1983) gives a very nice mechanical description of the mechanics of the behavior. It is essentially a random walk in three dimensions, where the time between tumbles is a Poisson random variable, governed by the direction that the bacteria is traveling. Bearon and Pedley (2000) argue that mean run time increases when a bacterium is moving up a chemoattractant gradient, a behavior known as chemotaxis. While chemotaxis behavior is not directly observed in flies, the modeling studies performed by Bearon and Pedley (2000), Othmer and Stevens (1997), and Grunbaum (2000) use techniques that I will emulate in my study of fruit fly foraging.
Chapter 2

Biological Background

An investigation into the foraging behavior of a swarm of fruit flies first requires a strong understanding of two elements of fruit fly behavior: social interaction and free flight characteristics. In this chapter, I will explain some of the Biology necessary to build a meaningful model of *Drosophila* swarming.

2.1 Collective Action

In the wild, it is easy to observe a group of fruit flies on a food source. The question is, however, is there much of a biological justification for the consideration of collective behavior? This question is taken up in Tinette et al. (2004), who observed collective action in swarms of *Drosophila*. Flies in their experiments did not individually assess all available food sources, but rather, food sources were located and tested by a few members of the swarm, and then the group aggregated on a favorable source.

The experiments in Tinette et al. (2004) were carried out in a clear box, where the location, strength, and quality of food sources could be changed as well as the amount and species composition of the flies used in the test. The food sources were contained in small glass containers, such that the experimenters could count the number of flies accessing a food source in any given trial. They found differences in the aggregation behaviors of certain mutant strains, but we need not be concerned with those differences in this project. Instead, I will focus on the general observations of the fruit fly.
2.1.1 Search-Aggregation Cycles

Tinette et al. (2004) observed two phases of fly behavior, the so-called *primer* and *follower* modes. These behaviors are disparate, and can be defined as follows:

**Primer:** A ‘primer’ fly goes in search of favorable food sources, testing various possibilities. Eventually, a primer fly will settle on a preferable source.

**Follower:** A following fly does not search for or evaluate possible food sources, but is visually attracted to other flies, particularly aggregations.

Biology suggests that these behaviors rely on different sensory systems for information. Tinette et al. (2004) indicate that the ‘follower’ behavior is vision-based, as flies demonstrate a powerful visual responses while in free flight. While searching behavior is partially dependent on visual cues for orientation purposes (see Frye et al. (2003)) it is primarily based on scents, known as chemoattractants.
2.1.2 Conditions for Collective Action

Fruit flies require certain conditions to participate in collective action as was observed by Tinette et al. (2004). Two that are interesting from the perspective of modeling are the dependence on the number of flies in the swarm and the saturation of the domain to be searched with scents from food sources. Tinnete et al. observed that the flies did not utilize the search-aggregation cycle when the number of flies was extremely low; with four flies in the test chamber there was no distinguishing between the flies’ behavior. The search-aggregation cycle, however, was clearly observed with 50 flies in the chamber, and most experiments were carried out for groups of 200 flies. The other condition of interest for the initiation of search-aggregation cycles was the presence of a scent gradient in the environment. When the environment was heavily saturated with chemoattractant, the flies did not participate in search-aggregation, but were inactive. The search-aggregation cycles were seen in environments where point sources created gradients in chemoattractant.

The search-aggregation method of foraging for food would presumably be advantageous because it requires less energy output from the swarm, as a few flies do the majority of the searching. In this thesis, I hope to gain a firm understanding of this behavior and some quantitative idea of its efficiency with regard to the energy used by the swarm during foraging. The modeling of a swarm, however, begins with the free flight characteristics of an individual.

2.2 Free Flight

Free flight by *Drosophila* has been the focus of quite a bit of experimental work of late, as researchers have tried to analyze the aerodynamics, energetics, control, and behavioral characteristics of fruit fly locomotion. These studies have motivated the creation of novel experimental techniques and interesting analysis. They have been particularly successful in recording the behavioral characteristics of *Drosophila* in free flight.

Fruit fly flight is characterized by a series of straight segments interrupted by rapid changes in horizontal heading known as saccades. A fly completes a saccade in ~ 50 – 100 milli-seconds, making the corresponding angular velocity is in excess of 1000 degrees per second (see Frye and Dickinson (2004)). A representative flight path is shown in Fig. 2.2. A fruit fly will generally turn through approximately 90 degrees during a saccade.
The direction that a fly turns (right or left) is seemingly at random, unless it is performing a collision avoiding maneuver. Flies tend to turn away from potential collisions. For instance, if a fly is approaching a wall on the left side, it will favor a saccade to the right. The length of time between saccades and correspondingly the length of the straight flight segments is also random, but can be influenced by environmental factors.

Figure 2.2: A sample of a flight of varying segment lengths interrupted by saccades. Note that turns are nearly 90 degrees at every saccade and that segment lengths are not constant. Frye and Dickinson (2004) observed that saccade angle in flies was normally distributed about 90 and -90 degrees when the fly was not performing a collision avoidance turn.

2.2.1 Odor Localization

Flies, like many animals, utilize scent to locate food sources in their vicinity. Odor localization by a fruit fly in free flight is important to understand, as it is the behavior that a model will have to consider for a fly in ‘primer’ mode. The flight path of a fruit fly participating in odor localization is still characterized by saccades of ~ 90 degrees, but in the vicinity of a chemoat-
A Flight Path Near a Food Source

Figure 2.3: A free flight path similar to those exhibited by flies in the vicinity of an odor source (red dot). Note that saccades tend to occur much more often in the vicinity of the odor source. This behavior is well observed in *Drosophila*. The end result is that a fruit fly in the vicinity of a food source will spend much more time close to that source than far away. Eventually, the source will enter the fly’s radius of detection and be found.

Tractant saccades occur more often and with smaller distances in between successive redirections. This was observed by Frye et al. (2003), using the same techniques that were developed to track normal free flight and introducing a hidden source of attractive scents in the floor of the test chamber. Fig 2.2.1 is an example of a free flight with saccading influenced by proximity to a food source, note that the fly spends much more time in the vicinity of the food source than in the far-field. I will suppose that flies exhibit similar behavior when in trying to swarm and in areas of high density.
2.2.2 Activity in Drosophila

The distributions of segment lengths in between saccades is not well studied. There is, however, some biological backing that says fruit fly activity demonstrates scalability in time. This means that descriptions of fruit fly activity look very similar at all scales. The experiment that led to the scalability conclusion is described in Cole (1995). Scalable activity can lead to flight lengths which are not distributed normally, but rather follow a power law distribution, so-called Lévy Flights, the properties of which will be examined in the following chapter.
Chapter 3

Lévy Flights and Searches

Lévy walks are a class of random walk, which are often found in biological behavior and are prevalent in foraging. I will use Lévy Flights to model the foraging behavior of fruit flies, as there is a significant biological justification to so and the behavior will correspond with the qualitative behavior descriptions from the past chapter.

3.1 The Lévy Flight

Lévy Flights, in this context, will be continuous time random walks in one dimension, where segment length between direction reversals, \( x \), is a random variable with the probability distribution function:

\[
p(x) = \begin{cases} 
0 & \text{if } x < x_{\text{min}} \\
cx^{-\mu} & \text{if } x \geq x_{\text{min}},
\end{cases}
\]  

(3.1)

where \( 1 < \mu \leq 3 \) and \( x_{\text{min}} > 0 \). The lower bound on \( \mu \) and the minimum segment length, \( x_{\text{min}} \), make the distribution normalizable, and hence a valid power-law probability density function (pdf). The parameter \( c \) is the normalizing constant and can be found from integration. For values of \( \mu > 3 \), the Central Limit Theorem says that over many iterations, the distribution of flight lengths will be normal. For \( 1 < \mu \leq 3 \), however, the Central Limit Theorem (CLT) is not valid and the distribution is upset by rare but extraordinarily long segment lengths. One of the requirements of the Central Limit Theorem is that the random variables have a finite second moment, according to Feller (1968). The Central Limit Theorem does not apply to random variables with power-law distributions with \( \mu \leq 3 \).
because they have infinite second moment, as follows:

\[ E[x^2] = \int_{x_{\text{max}}}^{\infty} x^2 p(x)dx \]
\[ = \int_{x_{\text{min}}}^{\infty} cx^{(2-\mu)}dx \]
\[ = \begin{cases} 
c\frac{x^{(3-\mu)}}{3-\mu} & \text{if } \mu > 3 \\
\infty & \text{if } \mu < 3.
\end{cases} \]

The infinite second moment of Lévy flights is the source of much of their interesting behavior. The Lévy flight formulation is not hard to extend to two dimensions, where coefficients and the limits of exponents are different, but the behavior’s properties remain. A characteristic Lévy flight in two dimensions is shown in Fig. 3.1.

Lévy flights give rise to counter-intuitive behavior, coming from the breakdown of the CLT. For instance, while processes which meet the hypothesis of the CLT lead to variance that scales linearly with time, variances in processes that display Lévy flights have other time-scaling behaviors, [Weeks et al. (1996)]:

\[ \sigma^2(t) \sim \begin{cases} 
t^2 & \text{if } 1 < \mu < 2, \\
t^{(4-\mu)} & \text{if } 2 < \mu < 3, \\
t & \text{if } \mu > 3.
\end{cases} \]

These scaling laws are in the regime of anomalous diffusion, where variance does not scale with time linearly, but with some power of time. In the case of Lévy flights, the transport is super-diffusive. The occasional very long flights undertaken by the walker cause it to move further from the origin, or other beings in a swarm, faster than a walker undergoing Brownian motion. This makes Lévy flights an ideal governing behavior for foraging for scarce resources.

### 3.2 Lévy Searches

Random walks are a common way to conceptualize searching behaviors in biology and other fields and Lévy flights are included in the classes of random searches that have been investigated. In fact, Lévy flights can be shown to be an ideal searching strategy for domains where resources are scarcely distributed.
Figure 3.1: A Lévy flight in two dimensions. Note that the flight path has a scalable nature, where the flights of similar length are clustered with very long flights separating them. If the image was viewed at a scale much further out, the entire path currently visible would be a single cluster within a much larger flight path. Given the scalability of *Drosophila* behavior, it is believed that fruit fly flight paths are actually Lévy in nature, as opposed to being distributed normally.
3.2.1 Unbiased Searches

Viswanathan et al. (1999) show that a random search governed by an inverse power law is optimal for values of $\mu$ which lead to Lévy flights. The argument is easy to see in one dimension. They let the segment lengths in a random walk be defined as in eq. 3.1, then a searcher behaves with the following rules:

1. The searcher begins a search by selecting a path direction randomly and a segment length from eq. 3.1.
2. If there is ever a target within a distance $r_v > 0$, then the searcher proceeds directly to the ‘found’ target. This is the radius of detection about the searcher.
3. If there is no target within $r_v$ of the searcher, then the searcher proceeds.
4. If the searcher travels the segment length selected in (1) without encountering a target, then it selects a new direction of travel and a new segment length randomly.

Viswanathan et al. (1999) then define the search efficiency $\eta(\mu)$ by

$$\eta(\mu) = \frac{1}{\langle l \rangle N}.$$ 

There, $\langle l \rangle$ is the mean segment length and $N$ is the mean number of flights taken by the searcher from one target to the next. They then distinguish two kinds of searches, destructive and nondestructive. Targets in destructive searches are destroyed after being visited by the searcher. Destructive searches are characterized by a larger mean number of inter-target steps,

$$N_d \sim (\lambda / r_v)^{\mu - 1},$$

where non-destructive searches are characterized by,

$$N_n \sim (\lambda / r_v)^{\mu - \frac{1}{\tau}}.$$ 

The parameter $\lambda$ is the mean free path of the searcher between targets, but can be thought of as the mean distance between target sites. $N_d > N_n$ because a searcher in a non-destructive search can turn back to a previously visited site, whereas a destructive searcher leaves a site empty, decreasing
the number of viable targets in the area. [Viswanathan et al. (1999)] show that for non-destructive searches $\eta(\mu)$ is maximized by choosing,

$$\mu = 2 - \frac{1}{[\ln (\lambda/r_v)]^2}.$$  (3.2)

Thus when the search is non-destructive, and $\lambda \gg r_v$ but not known, $\mu = 2$ is the optimal choice for a random search. Likewise, they show that for a destructive search, $\eta(t)$ has no maximum for allowable values of $\mu$, but efficiency increases as $\mu \to 1$. The reasons that Lévy searches are optimal when resources are scarce can be understood by the fact that the probability of returning to a previously visited site is lower for a Lévy searcher than a Gaussian one, and thus the Lévy searcher is more likely to visit new areas and find more targets. Similar results can be found for searchers who obey Lévy flights, but bias them either with *a priori* information about the distribution of walkers, or some environmental factor like a chemoattractant gradient.

### 3.2.2 Biased Searches - Length

[Marthaler et al. (2004)] investigate the effectiveness of Lévy searches where segment length is biased on *a priori* information. This is similar to the behavior that we see in fruit flies, where the animal preforms chemokinesis. In Marthaler et al., they analyzed a non-destructive search in two ways, where $\mu_1$ is calculated from the ideal search exponent defined by eq. 3.2 and where $\mu_2$ is calculated according to,

$$\mu_2 = H(\lambda(x) - r_v) \left( 1 + \frac{\max(P(x)) + 1}{\lambda(x) + 1} \right) + 3H(r_v - \lambda(x)),$$

when,

$$\lambda(x) = \int_{-\infty}^{\infty} |x - z|P(z)dz.$$

In the above, $P(x)$ is the probability of a local target at the point $x$, thus $\lambda(x)$ is an effective upper bound on the distance from the point $x$ to the nearest target. See that as $\lambda$ increases $\mu$ decreases and the forager takes generally longer steps as the density of targets decreases. The argument here is in one dimension, but if $x$ is thought of as a vector then the two-dimensional case is an easy extension. [Marthaler et al. (2004)] evaluated the efficiencies of the two choices for $\mu$ numerically and found that $\mu_2$ was much more efficient with respect to $\eta$. With one thousand targets in a domain 200 units
long and $r_v = 1.5$, $\eta_1 \approx 7$ and $\eta_2 \approx 33$. The second method is over three times as efficient. This seems odd, as $\mu_1$ was supposed to be optimal, but with increasing target density (falling $\lambda$) $\mu_1$ decreases and leads larger flight lengths, allowing the forager to ‘skip’ over targets.

### 3.2.3 Biased Searches - Direction

In the same paper [Marthaler et al. (2004)](#), Marthaler et al. also analyze searches where direction is biased by the distribution of sources, similar to an animal which would tend to turn up gradients. This behavior is not observed in fruit flies [Frye et al. (2003)](#), but is seen in some kinds of chemotaxis. They performed the same numerical analysis on a searcher with $\mu = 2$ and the probability of turning left or right dependent on the derivative $P_x$ of $P(x)$, where,

$$p_l = \begin{cases} 
.75 & \text{if } P_x < 0 \\
.50 & \text{if } P_x = 0 \\
.25 & \text{if } P_x > 0
\end{cases}$$

and,

$$p_r = 1 - p_l.$$

They found that the searched with biased direction was much more efficient, with $\eta \approx 55$. 
Chapter 4

Lagrangian to Eulerian Formulations

The flight path of a single fly participating in foraging behavior is not difficult to model (see Chapter 5). The questions then becomes, how can an individual-based model be altered such that it could be applied to an N-body swarm which will display behaviors similar to those seen experimentally? One route is to numerically simulate the swarm using a Lagrangian framework, but this is computationally intensive and I also want to build an Eulerian description of a swarm. By approaching the problem from both directions, I hope to better understand how the guiding questions for the thesis can be answered and see some interesting mathematics. In this chapter, I present several simple examples of ways by which an N-body system with certain rules for interaction can be modeled at the individual level, tracking position and velocity, and then described using a Eulerian PDE, focused on density and velocity fields.

4.1 A Simple Case

The process of relating a local model of a random walk for every member of a swarm to a PDE for the entire swarm is described by Othmer et al. (1988). They let a particle move along the x-axis with constant speed \( v \), and suppose that the particle randomly changes direction at intervals governed by a Poisson process with rate \( \lambda \). If \( p_r(x, t) \) and \( p_l(x, t) \) are the probability density of particles that are at \( (x, t) \) and are moving to the right and left,
respectively. These satisfy the system,
\[
\begin{align*}
\frac{\partial p_r}{\partial t} + s \frac{\partial p_r}{\partial x} &= -\lambda p_r + \lambda p_l \\
\frac{\partial p_l}{\partial t} - s \frac{\partial p_l}{\partial x} &= \lambda p_r - \lambda p_l
\end{align*}
\]
and their sum is the probability that a particle is at \((x, t)\). They then define the probability flux as,
\[
J \equiv s(p_l - p_r)
\]
Then, by taking the proper derivatives,
\[
\begin{align*}
\frac{\partial p}{\partial t} + \frac{\partial J}{\partial x} &= 0 \\
\frac{\partial J}{\partial t} + 2\lambda J &= -s^2 \frac{\partial^2 p}{\partial x^2}
\end{align*}
\]
Where \(p(x, 0)\) and \(J(x, 0)\) are defined by \(p_r(x, 0)\) and \(p_l(x, 0)\). By differentiation and substitution, these two can be combined to the hyperbolic system,
\[
\frac{\partial^2 p}{\partial t^2} + 2\lambda \frac{\partial^2 p}{\partial x^2} = s^2 \frac{\partial^2 p}{\partial x^2} \tag{4.1}
\]
with the initial conditions,
\[
p(x, 0) = p_0(x) \quad \text{and} \quad \frac{\partial p}{\partial t}(x, 0) = -\frac{\partial j_0}{\partial x}(x).
\]
Eq. [4.1] is the Telegrapher’s equation. The mean squared displacement for the system can be found by assuming that \(p(x, t)\) and its first two derivatives approach zero at \(|x| \to \infty\). Then with
\[
< x^2 > = \int_{-\infty}^{\infty} x^2 p(x) dx,
\]
it holds that
\[
\frac{d^2 < x^2 >}{dt^2} + 2\lambda \frac{d < x^2 >}{dt} = 2s^2,
\]
with homogeneous initial conditions. Thus,
\[
< x^2(t) > = \frac{s^2}{\lambda} \left( t - \frac{1}{2\lambda} (1 - e^{-2\lambda}) \right) .
\]
Thus,
\[
< x^2(t) > \sim \begin{cases} 
  \frac{s^2 t^2}{\lambda} & \text{for small } t \\
  \frac{\varepsilon^2}{t} & \text{for large } t.
\end{cases}
\]
In this example a behavior, which is simple at the individual level, leads to a PDE for the density of the swarm. The solution to that PDE looks like solutions to the diffusion equation for large values of \(t\), and the swarm disperses over the real line.
4.2 Extension to Density-Dependent Behaviors

The model presented for insect swarming in the above example is overly simplistic to well-describe a swarm. Most notably, it lacks any sort of interaction between swarm constituents. Grunbaum (1994) approaches interaction, translating a Lagrangian model into an Eulerian one. He assumes that at any given observation, individuals are distributed as a set of Poisson points according to the density distribution. In any spatial interval, under this assumption, the number of individuals is a Poisson distributed random variable.

4.2.1 Lagrangian Framework

Consider a one-dimensional swarm on the $x$-axis, where individual behavior is governed by two parameters, $\psi$ and $\mu$, the sensing distance and target density. Thus during the social behavior of an animal, the intervals of length $\psi$ on either side of the animal are tested for other individuals, and individuals move toward areas of density $\mu$. If $v_i$ is the number of individuals in a spatial interval $d_i$ (length $\psi$) then the local density for an animal at the point $x$ is,

$$\rho(x) = \frac{1 + v_1 + v_2}{2\psi}.\]

Grunbaum then creates a time dependent social forcing which is evaluated at random intervals at rate $\lambda_s$, governed by,

$$f_1(v_1,v_2) = \text{sgn}(2\psi\mu - 1 - v_1 - v_2)$$
$$f_2(v_2,v_2) = \text{sgn}(v_1 - v_2)$$
$$f_s(v_1,v_2) = f_1(v_1,v_2)f_2(v_1,v_2). \quad (4.2)$$

In addition, individuals are subject to a random Gaussian force, $f_r$, with mean 0 and variance $\sigma^2$ at random intervals with rate, $\lambda_r$. Individuals respond to the forcing, $F(t) = f_s + f_r$ according to Newton’s Law,

$$m\frac{d^2x}{dt^2} + d\left(\frac{dx}{dt} - U\right) = F(t),$$

where $d$ is the drag co-efficient and $U$ is advection due to an external flow field.
4.2.2 Eulerian Translation

Grunbaum (1994) defines a velocity autocorrelation and a power spectrum to derive the form of the Eulerian model. The velocity autocorrelation, $R_v(\tau)$ ($\tau$ is the non-dimensional time interval), and power spectrum, $S_v(\omega)$ are related by the Fourier transform. By transforming eq. 4.3 and applying various substitutions using the parameters of the swarm, one comes to the limiting expression,

$$R_v(\tau) = De^{-|\tau|} + (u + \gamma\phi(x,t))^2,$$

(4.4)

where $D$ is the diffusion coefficient for the expected density flux due to the random forcing, $\gamma$ is the characteristic velocity of the swarm, and $\phi(x,t)$ is the expected value of eq. 4.2, which takes the form,

$$\phi(x,t) = \sum_{v_1=0}^{\infty} \sum_{v_2=0}^{\infty} c(v_1, v_2)f(x, t, v_1, v_2).$$

(4.5)

Here, $c(v_1, v_2)$ is the joint distribution for $(v_1, v_2)$ about $x$ at time $t$. The assumption that the distribution of individuals in the swarm is a distribution of Poisson points says that $v_1$ and $v_2$ are independent, such that,

$$c(v_1, v_2) = c_1(v_1)c_2(v_2),$$

(4.6)

where $c_m(k)$ is the probability that there will be $k$ individuals in the interval $d_m$ with respect to $x$,

$$c_m(k) = e^{-\rho_m}\frac{\rho_m^k}{k!},$$

(4.7)

with,

$$\rho_m(x,t) = \int_{d_m} \rho(x',t)dx'.$$

(4.8)

Then, by eq. 4.4, the PDE that determines the density flux of individuals is

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} - \frac{\partial}{\partial x}[\rho(U + \gamma\phi(x,t))],$$

(4.9)

which becomes a nonlinear partial integro-differential equation upon substitution of eqs. 4.5, 4.6, 4.7 and 4.8. Grunbaum (1994) evaluates solutions to eq. 4.9 numerically, and finds that the solutions to the Eulerian formulation positively compare with simulations of the swarm from the Lagrangian perspective, which serves as his verification of the Poisson point assumption.
Chapter 5

A New Direction

5.1 Pursuit of a 1-D Lagrangian Model

A fairly simple Lagrangian model of fruit flies foraging in one spatial dimension can tell us quite a bit about the swarming of fruit flies and the search efficiency of a swarm based on its behavior. I have built such a model, which I will describe in the following sections.

The model that I have implemented describes the positions of $N$ 'bugs' by their positions on the line, $\vec{X}$, and a count-down clock for each, denoted by $\vec{\tau}$. In this model, a bug at position, $x_i$, will saccade if and only if $\tau_i = 0$. Upon saccade, $\tau_i$ will then bee reset according to some function, which incorporates the interaction with other flies and attraction to chemoattractants into the model. The condition that flies only saccade according to their internal timer means that the bugs only make decisions while saccading, which is not entirely physical, but is computationally easier than evaluating the fitness of the environment for each fly at each time-step. I will show later that this approach of evaluating the environment only during saccades results in similar results to more physical, integrative, models and biological experiments. In this model, the flies move with a constant speed, $c = 1$, and the time steps are normalized, such that the entries in $\vec{X}$ and $\vec{\tau}$ are always integer valued. Let $x_i^{n+1}$ denote the position of bug $i$ at time, $t = n + 1$, and similarly represent the internal clock, $\tau_i^{n+1}$, then the movement of the flies can be expressed by,

\[
\begin{align*}
    x_i^{n+1} &= x_i^n + c_i \\
    \tau_i^{n+1} &= \tau_i^n + F_i^n.
\end{align*}
\]

In the above system, $c_i$ can take on the values $c_i = \{-1, 1, 0\}$, which corre-
spond to moving left, right and staying in place, it’s value is a random variable set during the last saccade. The random variable, $F_i$, is used to change the internal clock of bug $i$ and has a large affect on individuals’ behavior. $F_i$ is a random variable whose value also depends on the last saccade by the conditions,

$$P\{F_i^n = -1|\tau_i^n > 0\} = 1 \quad (5.1)$$

$$P\{F_i^n = \tau_0|\tau_i^n = 0\} = f_i(\vec{X}, \tau_0), \quad (5.2)$$

where $\tau_0 > 0$. The probability density function, $f_i(\vec{X}, \tau_0)$, is the piece of the model by which it is easiest to change the behavior of the swarm, as it, along with $c_i$, determine the swarm constituents’ response to their environment and each other. In this section, I will develop a one dimensional model of fruit fly behavior, beginning with a group of Lévy walkers.

### 5.1.1 Base Case : Lévy Walks

As a validation of the model, we can look at the behavior of the swarm when $f_i(\vec{X}, \tau_0)$ takes the form of a Lévy distributed random variable,

$$f_i(\tau_0) = c\tau_0^{-\mu}. \quad (5.3)$$

In this case we would expect to see the behavior discussed in Chapter 3.

Figure 5.1 shows the mean, variance, skew, and kurtosis for three swarm simulations. These reflect the behavior we would expect to see from a swarm of non-interacting Lévy walkers in one dimension. The mean and skew are both near zero for each of the runs, which indicates no directional bias in saccade direction or length. The variance scales with a power of $t$. According to [Weeks et al. (1996)](Weeks1996), one would expect the variances to scale like $t^{1.68}$, where the proportionality constant would be $\approx 2.5$. Lastly, the kurtosis lines for the different simulations all indicate that the long term distribution of the swarm is leptokurtic (kurtosis is greater than 3), which essentially means that the distribution has a high point and long tails. Figure 5.2 shows the distribution at 4 time steps for the simulation in blue in Fig. 5.1.

### 5.1.2 The Next Step : Lévy Walkers and Attractors

Now consider the flies to have a run-and-tumble like behavior, where they are more likely to assume lower values of $\tau_0$ upon saccade while in some
Figure 5.1: This figure shows the [left to right; top to bottom] sample mean, variance, skew and kurtosis for three iterations of the model, where $N = 1000$ and $\mu = 2.32$. In these simulations, the initial condition was delta-like, with all of the bugs at the origin, and the simulations were run for 4000 time steps.

vicinity, $r_v$, of a food source. The $F_i$ will now depend on both $\tau_0$ and $x_{sink}$, the distance to the nearest food source, by,

$$F_i = \begin{cases} \frac{x_{sink}}{r_v} \tau_0, & \text{if } x_{sink} \leq r_v \\
\tau_0, & \text{otherwise,} \end{cases}$$

where the p.d.f for $\tau_0$ remains as it was in eq. 5.3. I chose this function for $F_i$ because it allows for the flies to become more ‘excited’ about environments closer to an attractant and to not saccade once they reach the food source.
Figure 5.2: This figure shows 100-bin histograms of bug position for the blue simulation in Fig. 5.1 for 4 time steps. The delta-like initial condition would appear as a bar of height 1000 at the origin and is not pictured. Note both the heavy-tailed nature of the distribution and the height of the enter in the T = 4000 frame.
Figure 5.3 shows the moments for three swarm simulations with attractants, along with a reference case from the last section. In these cases, the overall swarm behavior is similar to that from the first case. The mean position of the swarm, and the skewness of their distribution, are both close to zero. The variances for the swarms is scaling appropriately for Lévy walkers and despite the fact that saccades made within $r_v$ of the food sources are characterized by decreased length the swarms’ behavior remains super-diffusive. Lastly, the kurtosis of each simulation is what would be expected.
Figure 5.4: This figure shows histograms for simulations where the sink was located at $x = 100$ (left) and $x = 1000$ (right). The distribution on the left was taken at $T = 4000$, the final time step shown in Fig. 5.3. It clearly shows a large population of bugs near the attractant. Likewise, the distribution at the left shows a high concentration of bugs about the sink. This distribution was binned at $T = 5 \times 10^{-4}$.

Note that the kurtosis for the red simulation (sink at $x = 100$) is higher, probably because of a large number of bugs near the sink. Since that simulation has the sink closest to the origin, it is expected that more bugs will fall into the attractor over a similar amount of time. A high concentration of near $x = 100$ also explains the slightly lower variance seen in this second case. Figure 5.4 validates that there is a large grouping about the sink, when $x = 100$, at later times. It also shows that a similar grouping will occur when the sink is far from the origin, $x = 1000$, but that it takes much more time to develop. The time lag makes the $x = 1000$ and $-300$ cases look similar to the regular random walk with respect to the overall swarm characteristics. Interaction terms, however, will change the large-scale swarm dynamics more significantly.

### 5.1.3 An Appropriate Model: Directionally Interacting Lévy Walkers with Sinks

The last model had flies gather in some number about food sources, but excluded what we saw in Chapter 2 regarding the interaction between flies and cooperative foraging. We seek a model that will combine the attraction that we implemented in the last section with a way for flies to choose the direction of their saccades based on the positions of the other members of the swarm and their path length based on the local swarm density. In order to
do this, I calculate a version of the Morse potential, usually seen in potential energies of diatomic molecules, as a measure of the force the swarm has on an individual. My version of the Morse potential is directional meaning I calculate it on the left and right, by
\[
M_l = \sum_j e^{-|x_i - x_j|}
\]
\[
M_r = \sum_k e^{-|x_i - x_k|}.
\]
In the above equations, \(j\) is the set of indexes for bugs to the left of the bug whose potential is being calculated and \(k\) indexes the bugs to the right. The total Morse potential is calculated by,
\[
M_0 = M_l + M_r.
\]
The use of exponential forces, such as the Morse potential that I have defined above, is a common technique in swarm modeling. Mogilner et al. (2003) use an exponential forcing and investigate its effect on the swarm shape and cohesiveness. Usually, the pairwise interaction is calculated with another term, with a different sign in the exponent, so that a pair can have a "comfortable" distance for which their pairwise potential energy is zero. I do not use this technique here, because it would force a non-physical interaction between bugs which are close on the line. This interaction is usually imposed to model collision avoidance, but since the bugs in this model must collide, we ignore the repulsive term and calculate the attractive one.

This is the first model in this chapter that uses the model state to influence the direction that flies turn while in the swarm. Thus there are three behaviors that the flies in this model must exhibit while saccading, beyond those of the standard random walker.

1. When a fly is within \(r_v > 0\) of a food source, then the length of flight segments will depend linearly on the distance between that fly and the food source.

2. A fly should choose the direction which exhibits the higher Morse Potential most of the time.

3. A fly will limit its flight length when its total Morse Potential is higher than some minimum value, to encourage ‘packets’ of flies.

The model’s parameter, \(F_i\) can be written as follows,
\[
F_i = g(\bar{X})h(x_{sink})\tau_0, \text{ for } \tau = 0.
\]
In this formulation, \( g(\vec{X}) \) gives the flight length dependence on the total morse potential by a step function

\[
g(\vec{X}) = \begin{cases} 
1/10, & \text{if } M_i > M_0 \\
1, & \text{otherwise}
\end{cases}
\]

where,

\[ M_i = \sum_{j \neq i} e^{-|x_i - x_j|}. \]

Then I use the same function for \( h \) as we did in the last section, such that

\[
h(x_{sink}) = \begin{cases} 
x_{sink} \frac{x}{r_0}, & \text{if } x_{sink} \leq r_0 \\
1, & \text{otherwise}
\end{cases}
\]

where \( x_{sink} \) is the distance to the nearest food source. \( \tau_0 \) is still distributed with the inverse power law that defines a Lévy walk. Lastly, \( c_i \) depends on \( \vec{X} \) by the following:

\[
P\{c_i = 1 | M_{i,+} > M_{i,-}\} = 0.9
\]
\[
P\{c_i = 1 | M_{i,+} = M_{i,-}\} = 0.5
\]
\[
P\{c_i = 1 | M_{i,+} < M_{i,-}\} = 0.1
\]

and

\[
P\{c_i = -1\} = 1 - P\{c_i = 1\}.
\]

This formulation allows the two dependencies, to interact and keep flies in highly desirable areas. I decided to make the dependence on the left and right Morse potentials \( (M_{i,+} \text{ and } M_{i,-}) \) non-deterministic to perhaps better reflect the behavior one might actually see in a swarm. Fig. 5.5 shows the moments for simulations with various values of \( M_0 \). In this figure, there are several interesting differences in the swarm moments that were not observed in the previous cases. Chiefly, in this set of simulations, we see a large difference in the swarm variance for different values of \( M_0 \). For low values of \( M_0 \), the swarm remains cohesive through time, and has half the variance of both the large \( M_0 \) simulations and the previous cases. This cohesiveness indicates that the swarm spends much of the time near the critical values of \( M_0 \) and a large proportion of the flight lengths are smaller. Figure 5.6 shows the positions of the bugs at the final time for the \( M_0 = 5 \) and 200 simulations. The histograms of position and the swarm...
Swarm Moments for the Interacting Swarm

Figure 5.5: The swarm properties for the directionally interacting swarm are shown in this figure. In those simulations, a sink was located at \( x = 100 \) and \( M_0 = \{5, 8, 25, 200\} \), corresponding to the blue, red, green and black lines, respectively. As before, \( N = 1000 \) and time was recorded for 4000 steps.
moments show that there is interesting behavior going on within these swarms. Figure 5.7 shows the evolution of a swarm operating under the full set of behavioral rules, where the bin with the highest number of flies moves from around the origin to the area around the sink.

The time series for simulations with different values of $M_0$ look similar to the $M_0 = 25$ case shown above. To better understand how these various modeling techniques work, we can look at their various search efficiencies.

5.2 Search Efficiencies of the 1-D Schemes

In a Lagrangian setting, it is easy to look at search efficiency as a function of the model parameters. I have placed bugs with the same behavioral characteristics I introduced in the last section in a finite domain with periodic boundary conditions. When a fly reaches $x_{i}^{n} = \pm L$, then $x_{i}^{n+1} = \mp L$. The finite domain is more physical, in that flies can only move so far before starving or perhaps entering another foraging swarm, and makes the problem easier computationally. Since flies cannot move off to infinity, they must eventually interact with the attractant. Additionally, when flies saccade within $r_{s} > 0$ of the sink, they stop moving and ”stick” in that position, having found the sink. Figures 5.8 and 5.9 shows the search efficiency of the 3 models. These examples show that a strategy where each actor is searching are much faster $\approx 2x$ than flies on a random walk, without any environmental or interaction effects. Likewise, the directionally-interacting models are faster than the model featuring only the searching flies. The
Search Efficiencies of the 1-D Schemes

Figure 5.7: This figure shows the group of flies on a food source grow with time. It is the histogram time series for the green simulation from Fig. 5.5. The growth of the bin above $x = 100$ shows the effectiveness of the search strategy, as the point of highest density migrates from the origin, where the bugs were initialized.

The mean times to having great than 75% of the swarm located for the simulations illustrated above are,

$$\begin{align*}
\text{Random} & \sim 22582, \\
\text{Attractant} & \sim 11686, \\
M_0 = 200 & \sim 7051, \\
M_0 = 25 & \sim 6972.
\end{align*}$$

From those limited samples, it appears that the search efficiency is practically the same for the two full models with the spatial parameters im-
Figure 5.8: This figure shows the percentage of bugs that have found and landed on the food source vs time step, for 4 versions of the 1-D model and 5 runs of the simulation each. For each simulation, the attractor was located at $x = 100$, $L = 500$, $r_s = 5$, and $X(0) = 0$. In the top, the bugs are simply Lévy walkers. The simulation shown on the bottom is for the bugs with an attractor. Note the differing scales in time, which show the efficiency of the swarms.
Figure 5.9: This figure shows the search efficiencies for 5 directionally-interacting swarms with attractants. The $M_0 = 25$ and 200 simulations are ordered top to bottom. The horizontal scales are the same for these two plots, meaning that their efficiencies are similar, with $M_0 = 25$ swarms seeming to be a little quicker.
plemented with that set of spatial parameters (values of $L$ and $r_s$). The $M_0 = 25$ runs, however, display more variance than the $M_0 = 200$ simulations. I believe that an interesting extension of this work would be to investigate the efficiency of the full model over a parameter space with ranging values of $M_0$ and $r_s/L$.

5.2.1 Interpretation and Possible Extensions

The full model of a directionally-interacting swarm seems to reflect the dynamics of actual swarms of searchers fairly well. The governing rules do not create a bias in direction for the swarm in the case where food sources are far away from the swarm or non-existent, the walkers still diffuse as would be expected from a Lévy Walk, and the full model is able to complete searches faster than if each bug were to find the food source on its own. This model may also be exposing some interesting behavior, which might warrant further investigation. First, it seems like bugs in the full model who end up far from the origin, and food sources, tend to be grouped relatively closely with respect to their distance from their initial position. This is evident in the long-time histograms, where there will be a bin with several flies in it far from the origin, see Figs. 5.6 and 5.7. It would be interesting to see whether these smaller swarms, or packets, form early and then diffuse out, aggregate in the far field, or some combination of both. These groups could take the ‘primer’ and ‘follower’ behavior to another scale, where they actually move the entire swarm out of its immediate area. In a sense, these packets might be why a swarm moves from the kitchen to the back porch.

5.3 The One Dimensional Eulerian Framework

The Lagrangian formulation in the last section is numerically convenient, being both fast in computation and easily traceable, but as I showed in Chapter 4, it can be helpful to have an Eulerian formulation of the model to provide model validation and analytical results. In this section, I will derive the equations of motion for the continuum case of the model presented in the last section of the chapter.

The continuum version of my one dimensional model closely reflects the models built by Grunbaum (2000), where the continuum approximation of bugs moving in one dimension is also governed by an internal state, such as satisfaction with the environment. In this case, however, the internal state is the countdown clock, $\tau$, which actually measures a fly’s satisfaction
with its environment at the time and position of the last saccade. This will lead to some interesting governing equations, which will take the form of partial integro-differential equations.

To begin, let $\rho(x, t, \tau)$ be the density of bugs at position $x$ and time $t$ with $\tau$ time left until a saccade. Then consider both the left- and right-moving densities, $r(x, t, \tau)$ and $l(x, t, \tau)$, which move with speed $c$ and satisfy,

$$\rho(x, t, \tau) = r(x, t, \tau) + l(x, t, \tau),$$

and,

$$\int \rho(x, t, \tau) d\tau = \rho(x, t).$$

Now consider a rectangle of size $\Delta x$ by $\Delta \tau$, placed somewhere in the upper half plane created when $x \in \mathbb{R}$ and $\tau > 0$, as pictured in Figure 5.10. Due

Fluxes in the Continuum Case

![Figure 5.10: The diagram shows the fluxes in and out of the rectangle with time. The characteristics move down in $\tau$ and right or left, depending on which population is being tracked. In addition, density which reaches the $\tau = 0$ line at $(x_0, t_0)$ is redistributed to $r(x_0, t_0, \tau)$ and $l(x_0, t_0, \tau)$ with some probabilities.](image)
to the complicated fluxes for a stationary rectangle it is best to consider a rectangle which travels with the characteristics, and exploit the material derivative to say that, for the right-moving density,

\[
\frac{Dr}{Dt} = F(\rho, x, t, \tau),
\]

where \(F(\rho, x, t, \tau)\) is the redistribution function, which carries mass from the \(x\)-axis back into the domain. Then, by the definition of the total derivative,

\[
\frac{Dr}{Dt} = \frac{\partial r}{\partial t} + c \frac{\partial r}{\partial x} - \frac{\partial r}{\partial \tau}.
\]

Thus for \(r(x, t, \tau)\) and \(l(x, t, \tau)\),

\[
\frac{\partial r}{\partial t} + c \frac{\partial r}{\partial x} - \frac{\partial r}{\partial \tau} = F_r(\rho, x, t, \tau)
\]

\[
\frac{\partial l}{\partial t} - c \frac{\partial l}{\partial x} - \frac{\partial l}{\partial \tau} = F_l(\rho, x, t, \tau).
\]

The theory on random walks governed by jumps in an internal state presented by Grunbaum (2000) predicts this system of equations. He starts with a system of the form,

\[
\frac{\partial r}{\partial t} + c \frac{\partial r}{\partial x} - \frac{\partial}{\partial \tau} (f_r r) = \lambda(\tau)(l - r) - \alpha(\tau) r + \int_{0}^{\tau} \alpha(\tau') r(\tau') T(\tau, \tau') d\tau'
\]

\[
\frac{\partial l}{\partial t} + c \frac{\partial l}{\partial x} - \frac{\partial}{\partial \tau} (f_l l) = \lambda(\tau)(r - l) - \alpha(\tau) l + \int_{0}^{\tau} \alpha(\tau') l(\tau') T(\tau, \tau') d\tau'.
\]

In the above, \(\lambda\) is the turning rate for bugs at \(\tau\), \(\alpha\) is the rate at which jumps in \(\tau\) occur, \(f_r\) and \(f_l\) are operators which alter the rate of change of \(\tau\) in time, and \(T(\tau, \tau')\) is the transition probability from \(\tau'\) to \(\tau\), given that a transition occurs, where,

\[
\int_{0}^{\infty} T(\tau, \tau') d\tau = 1.
\]

In the model that I have built, Grunbaum’s model is reduced by,

\[
\lambda(\tau) = 0 \text{ for } \tau > 0,
\]

\[
\alpha(\tau) = 0 \text{ for } \tau > 0,
\]
when $\tau > 0$ and $f_l = f_r = 0$. Then since $x(\tau) = \delta$, the integral simply samples the transition probability, to yield the system seen in 5.4 where,

$$F_r(x, t, \tau) = [r(x, t, 0) + l(x, t, 0)]T_r(\tau, 0),$$
and similarly for $F_l$. Hence, $F_r$ and $F_l$ can be interpreted as the transition probabilities for the total density at the $x$-axis as it is distributed into the right- and left-traveling densities through $\tau$. In the simplest case, where the bugs in the Lagrangian simulation would be on Lévy Walks,

$$F_r(x, t, \tau) = F_l(x, t, \tau) = \frac{c}{2} \tau^{-\mu},$$

when $\tau > \tau_{\text{min}}$. In the cases where the behavior rules are more complicated, the function $F$ takes on some interesting forms. For the model of foraging Lévy Walkers, that do not interact but are attracted to a sink as I described in Sec. 5.1.2,

$$F_r(x, t, \tau) = F_l(x, t, \tau) = \begin{cases} \frac{c}{2} \tau^{-\mu}, & \text{for } |x - x_{\text{sink}}| > r_v \\ \frac{c}{2} \left(\frac{r_v}{|x - x_{\text{sink}}|}\right)^{-\mu}, & \text{for } |x - x_{\text{sink}}| < r_v, \end{cases}$$

where $r_v > 0$ is the vision radius of the bugs and $x_{\text{sink}}$ is the position of the nearest food source. This function redistributes density on the $\tau = 0$ boundary to lower values of $\tau$ for points within the viewing radius of a food source. Lastly, we can look at the full model for a directionally interacting swarm, where for the right-traveling case,

$$F_r(x, t, \tau) = P \left(SM\tau\right)^\mu,$$

where,

$$P = \begin{cases} 0.9, & \text{if } M_r > M_l \\ 0.5, & \text{if } M_r = M_l \\ 0.1, & \text{otherwise}, \end{cases}$$

and

$$M_l = \int_0^x \int_0^\infty \rho(x', t, \tau) e^{-(|x-x'|)} d\tau' dx',$$

$$M_r = \int_0^\infty \int_0^\infty \rho(x', t, \tau) e^{-(|x-x'|)} d\tau' dx'.$$

$S$ reflects the dynamics of being near a sink, and takes a simple form,

$$S = \begin{cases} 1, & \text{if } |x - x_{\text{sink}}| > r_v \\ \frac{r_v}{|x - x_{\text{sink}}|}, & \text{otherwise}. \end{cases}$$
Lastly, the function $M$ gives the dependency on the total Morse potential by,

$$ M = \begin{cases} 1, & \text{if } (M_l + M_r) < M_0 \\ 10, & \text{otherwise.} \end{cases} $$

The function $M$ forces the distributive function, $F$, to spread more of the saccading density at low values of $\tau$ when the total Morse potential exceeds its critical value. The model, a combination of the equations listed over the last page, is now a partial integro-differential equation. Further study in this area will have to develop solution techniques for this type of equation, either analytical or numerical approximations, to validate the Lagrangian model.

### 5.4 Lagrangian Modeling in Two Dimensions

The extension of the Lagrangian model in one dimension to two spatial dimensions is easy to make and biologically relevant. The interesting foraging behavior exhibited by fruit flies occurs in the horizontal plane, as saccading is usually confined to the plane. Thus the two-dimensional version of my model will allow for comparisons between my numerical results to the data presented by Frye et al. (2003) and for easier interpretation of the numerical output. The model remains essentially the same as the version shown earlier in this chapter, only scalar position and velocity are replaced with vector quantities. The transition to two dimensions adds complexity to the turns that accompany saccades. In the one-dimensional model, a saccading fly either did not change direction or turned in the opposite direction. In the two-dimensional model, turns are sampled from identical normal distributions about $\pm 90$ degrees. A sample flight path is shown in Fig. 5.11. In that simulation, the fly is constrained to the arena outlined in red and will saccade away from the wall when it gets close, mimicking biological behavior. I designed these simulations to reflect, as closely as possible, the arena tests performed by Frye et al. (2003), to provide at least a heuristic validation of the model for individual free flight. Frye et al. (2003) develop an integrative model for a fly in an arena, where the probability of saccade is evaluated at each time step, and it favorably compared to the biological behavior. Thus, I have created Figure 5.12 to show the similarities between the two modeling techniques, and the similarity between my model and the biology. Further study of this two-dimensional model will have to include investigations on the role of interaction in two dimensions.
Figure 5.11: This figure shows the flight path of a foraging fly attracted to the food source at the blue circle. Note the number of saccades near the food source as opposed to other parts of the arena.

on swarm cohesiveness and search efficiency.
Figure 5.12: This figure shows the percentage of time spent in each cell over a simulation of length 40,000. In this simulation, one bug foraged through the flight arena for a food source located at $\mathbf{x}_{\text{sink}} = (-30, 20)$. The bug moved with speed $c = 30$, its initial position was assigned randomly, $\mu = 2.32$, and $r_v = 50$. This image compares favorably with similar figures from Frye et al. (2003).
Chapter 6

Conclusions

With this thesis, I investigated Lagrangian and Eulerian descriptions of insect swarms. The individual-based Lagrangian techniques are fit primarily for numerical, stochastic, simulation. Alternatively, the continuum-reminiscent Eulerian descriptions are difficult to solve, either analytically or numerically. These descriptions do, however, provide information that is much more general to specific swarm behaviors than the Lagrangian techniques. In the course of my investigation, I focused my energy on the swarming behavior of the fruit fly, *drosophila melanogaster* because it involved the combination of two interesting behaviors, saccading flight patterns and collective searching. Behavioral studies of *drosophila* demonstrate these two behaviors and I attempted to build a reasonable modeling technique to both reflect and combine these behaviors. I found that the flight of fruit flies, either individual or in a group, could be modeled as a random walk process governed by an internal clock, which counts down to the next saccade. From the biological information available, these models appear to be valid. Increasing saccade frequency near food sources, and thus decreasing the length of inter-saccade flights, results in a fly spending much more time in the vicinity of a food source and also allows a swarm of flies to find a food source in less time than it takes a swarm of flies which do not decrease their flight lengths. Likewise, decreasing inter-saccade flight length in areas of high Morse potential simulates the interaction that leads to swarm formation. Turning which is influenced by Morse potential also contributes to the swarming behavior. The increase in search efficiency seen when flies interact directionally and with food sources reflects the biological results of Tinette et al. (2004).

This project has raised more questions than it has answered. In building a
Conclusions

successful model, I have prepared a technique by which we can now study how the different parameters in my models, such as $M_0$, $r_v$, $\mu$, and $N$ – the critical Morse potential, flies’ vision radius, the Lévy parameter, and the swarm size – affect the behavior of the swarm both in search efficiency and shape. I believe there are four directions that future research on this project will proceed along,

1. A full parameter space investigation of the models introduced above.

2. Development of an approximation method for the continuum model which will serve to validate the Lagrangian results.

3. Numerical experiments with multiple food sources of varying qualities in the domain of a swarm, looking for the behaviors described by Tinette et al. (2004).

4. Investigations into the behavior of flies undertaking long walks from the swarm, either individually or in small packets, and what conditions lead to these flights.
Bibliography


