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### Simulating Polistes Dominulus Nest-Building Heuristics with Deterministic and Markovian Properties

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Simulating *Polistes Dominulus* Nest-Building Heuristics with Deterministic and  
Markovian Properties

by

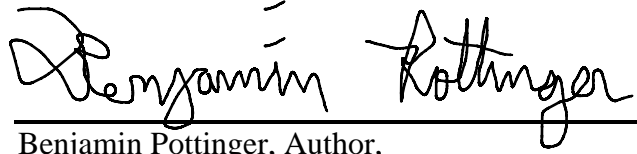
Benjamin Pottinger

A Thesis  
Submitted to the Honors College of  
East Tennessee State University  
in Partial Fulfillment  
of Honors Requirements

May 2022



Approved by:

A handwritten signature in black ink that reads "Benjamin Pottinger". The signature is fluid and cursive, with the first name being more prominent.

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Benjamin Pottinger, Author,  
Department of Computing

A handwritten signature in blue ink that reads "Matt Harrison". The signature is cursive and flows from left to right.

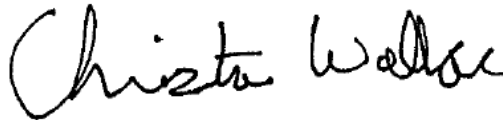
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A handwritten signature in black ink that reads "Istvan Karsai". The signature is bold and somewhat stylized, with the first name being very large.

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Dr. Istvan Karsai, Ph.D., Thesis Co-Advisor  
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A handwritten signature in black ink that reads "Christopher Wallace". The signature is cursive and elegant, with the first name being more prominent.

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Dr. Christopher Wallace, Ph.D., Thesis Co-Advisor  
Department of Computing

## ABSTRACT

European Paper Wasps (*Polistes dominula*) are social insects that build round, symmetrical nests. Current models indicate that these wasps develop colonies by following simple heuristics based on nest stimuli. Computer simulations can model wasp behavior to imitate natural nest building. This research investigated various building heuristics through a novel Markov-based simulation. The simulation used a hexagonal grid to build cells based on the building rule supplied to the agent. Nest data was compared with natural data and through visual inspection. Larger nests were found to be less compact for the rules simulated.

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## CHAPTER I: INTRODUCTION

Social insects collaborate to create complex structures. Downing and Jeanne hypothesized that wasps used “blueprints” to create nests: i.e., that worker wasps construct nests based on a predetermined idea of how nests should look (1988). This idea is intuitive, since wasps’ nests are almost perfectly symmetrical, which is economically efficient due to their use of less building material. This theory implies that wasps collaborate based on advanced knowledge and communication networks.

Indirect coordination and interaction have been proposed as driving mechanisms in wasp nest construction. (Karsai and Penzes, 1993) (Harrison, 2018) In this theory, wasps’ interactions with nests provide stimuli for heuristic decisions. This theory assumes that wasps lack the intelligence to understand how a nest should look upon completion but follow “rules of thumb” to create symmetrical nest shapes. (Karsai and Penzes, 1993)

These observations lead to questions as to what heuristics wasps use to build nests and what stimuli affect these decisions. Computer simulations allow researchers to correlate abstract models of wasp behavior with naturally observed colonies. Other considerations, such as foraging activities that occur away from the nest, can be abstracted in these models (Karsai and Penzes, 2000). Investigating paper wasps with simulations has the potential to give insight into how “dumb” social insects create advanced colonies.

Computer simulations have been built in the past to investigate the heuristics that govern wasp behavior (Adeo, 2010) (Harrison, 2018); however, past simulations have been restricted to smaller nest colonies due to hardware constraints; the value of different

heuristics can be more thoroughly understood with larger nests. This experiment trained nest-building heuristics proposed in earlier work with larger upper limits; furthermore, Markov chains were used to investigate these heuristics.

## CHAPTER II: BACKGROUND

### 2.1: Stigmergy

To understand how wasps build their nests, it's important to understand what mechanisms influence their behavior. In (1993), Karsai and Penzes discuss their research into the factors that determine how members of the *Polistes dominulus* wasp species build combs during nest construction. Karsai and Penzes modeled nest-building using a self-organized (or stigmergic [sic]) model. Wasp behavior is guided through stigmergy, “a mechanism of indirect coordination, through the environment, between agents or actions.” (Marsh and Onof, 2007) Wasp behavior during nest construction is influenced by stimuli left by other wasps—a form of decentralized communication that lacks a central command or hierarchy. This model assumes that wasps determine where and how to build cells through interaction with the nest structure instead of interaction with other wasps.

### 2.2: Rules of thumb

In (2000), Karsai and Penzes explore “rules of thumb” that wasps use to approximate ideal behavior when constructing nests. Wasp behavior is guided through stigmergy. Wasp behavior during nest construction is influenced by stimuli left by other wasps—a form of decentralized communication that lacks a central command or hierarchy. The aim of this research “beyond examining the optimality of round one-comb nests in regard to material economy and structural compactness, was to explore the predictive power of simple stigmergic [sic] rules of thumb that may be used by builders in *Polistes dominulus* Christ colonies.” The research distinguished between “ideal” (or most symmetrical) and naturally observed nest shapes. Through the testing of different

building algorithms that use prospective rules of thumb, the authors sought to replicate naturally observed wasp behavior.

For this research, the authors focused on modeling embryonic-stage (queen-wasp-stage) nest building, which entailed one agent representing the queen wasp and a maximum of fifteen cells. The nest was modeled using a two-dimensional plane. The authors assumed that wasps place new cells next to at least two pre-existing walls to decrease costs in building material; that cell initiation is a local decision, meaning that wasps typically limit checks to one cell and its neighbors; and that choices among multiple cell initiation locations with two pre-existing walls were random. Finally, the model was limited to two considerations: the nest in its current configuration and the building algorithm that predicts the next move.

Karsai and Penzes (2000) observed that naturally occurring wasp nests do not fully optimize the use of building materials. An optimal nest form maximizes nest compactness, or geometric compression and symmetry. With three exceptions, all nest configurations observed in nature were the most compact. According to the authors, these naturally occurring imperfections are due to wasps' use of heuristics, which yield good but not necessarily ideal nest forms.

Several rules were proposed as models for choosing where to construct new cells. One, MaxW, puts each new cell at a site with the highest number of pre-existing walls. This rule generated many forms not observed in nature and was discarded as a prediction algorithm. A second, MaxAo, placed each new cell next to the nest's oldest cell. This rule failed to generate the nonoptimal forms observed in nature. The most successful, SumAMax, placed new cells at locations that maximized the combined age of

neighboring cells SumAMax differed from MaxAo in that it “integrates (sums) the stimuli for a given position rather than seek a mere maximum irrespective of the current configuration.” This algorithm predicted the most natural and compact forms with only one additional form.

Karsai and Penzes (2000) also observed that the stimuli that govern how wasps build nests are not properly understood. At one time, it was assumed that the stimuli were obtained primarily through wall rules and cell age. These additional stimuli could be a chemical that is more prominent in older cells than younger cells. While the SumAMax rule was the best fit for observed behavior, other rules may be needed to model how nests grows beyond the embryonic stage. Larger nests exhibit more nonoptimal forms, possibly because wasps do not check every position as the nest passes a certain threshold in size.

### **2.3: Nest metrics**

Karsai and Penzes (1996) quantified a nest’s structure in terms of its compactness, potentially buildable cells, diameter ratio, height, and eccentricity. Compactness was defined as a nest’s degree of symmetry. Potentially buildable cells were defined as potential positions for cell initiation that met the authors’ postulated constraints for building cells. For example, one constraint observed in nature is that wasps place new cells in positions with three or more pre-existing walls. This rule decreases the number of possible cell initiation locations. Diameter ratio measures a nest’s elongatedness [sic], or ratio of width to height. Height is the length of the structure’s longest cell; it appears to be independent of nest length and size. Eccentricity is the degree to which cells are distributed unevenly around the nest’s topological center.

Compactness as a metric to distinguish unique nests has evolved over time since its inception in Karsai and Penzes' research (1996). In this study, the metric was derived through finding the square root of the sum of squared distances of the coordinates of each cell and the nest's geometric center. (Equation 1) This equation calculates nest location through rectangular coordinates that require a square root of three calculation due to the triangle-based geometry of the nest's hexagonal grid.

*Equation 1: Original compactness equation with rectangular coordinates.*

$$C_R = \sum_i \sqrt{(x_i - x_e)^2 + (y_i - y_e)^2}$$

*Equation 2: Variable formulas for rectangular coordinates.*

$$(x_e = \frac{1}{N} \times \sum_i x_i, y_e = \frac{1}{N} \times \sum_i y_i)$$

In (2018), Harrison reduced the computational resources needed to calculate nest compactness. He used three coordinates to represent the hexagonal grid, adding an extra dimension to the grid. This new equation removes the irrational coefficient without a loss in accuracy. Unlike the rectangular grid, the equation adds a third variable that represents the z-axis (Equation 2).

*Equation 3: Modified compactness equation for hexagonal coordinates.*

$$C_H = \sum_i \sqrt{(x_i - x_e)^2 + (y_i - y_e)^2 + (z_i - z_e)^2}$$

*Equation 4: Variable formulas for hexagonal coordinates.*

$$(x_e = \frac{1}{N} \times \sum_i x_i, y_e = \frac{1}{N} \times \sum_i y_i, z_e = \frac{1}{N} \times \sum_i z_i)$$

## 2.4: Markovian model

In computer science, a Markov chain is a “stochastic model describing a sequence of possible events in which the probability of each event depends only on the state attained in the previous event.” (Gagniuc, 2017) The Markov chain model enables an exploration of all branches of a decision tree. A practical example of Markov chains is Google’s PageRank which allocates search rankings for pages based on the frequency of their visits. Markov chains are versatile for traversing between states in a decision space in which the desired behavior is unknown or unpredictable. The transitions between states are determined based on tunable parameters.

It so happens that Markov chains are ideal to test nest-building heuristics and capture all unique nests they predict. The algorithm is assigned a heuristic and the heuristics will narrow the decision space to those which meet the conditions of the heuristic in use. In this framework, it is possible to capture the nest permutations of different heuristics.

## **CHAPTER III: METHODS**

### **3.1: Reviewing the code of previous models**

In Harrison (2018), a three-dimensional simulation was built in Microsoft Visual Studio and C++. The simulation was built with three-dimensional visualization in mind; however, the architecture required for a Markovian and modular heuristics-based simulation would necessitate a large refactor. The decision was made to create a new simulation in C#. Before beginning on a simulation, a thorough review of the 2018 simulation was conducted. This review comprised reviewing the code, model assumptions, and design decisions. Some areas were identified that could be modified and reconsidered for the sake of this simulation. More specifically, the relationship between certain model elements such as the nest, nest cells, and cell walls were reconsidered to be more modular. With this review completed and our goals defined, the experiment was ready for the first phase of development.

### **3.2: Nest permutations generation**

The first iteration of the simulation was a brute force simulation to test if the basic features were implemented as planned. This program consisted of nest, cell, and wall classes to model the nest, and a main class to generate all possible configurations of the nest up to a variable upper limit. This experiment, furthermore, tested compactness as the mechanism for distinguishing between unique nests. This unique nest data was compared with Harrison (2018), Karsai and Penzes (2000), and Adoe (2011) data to ensure that our results are consistent with theirs and reflect prior studies on the efficacy of compactness. This first iteration can print these nests to a CSV file for visual inspection. The CSV tool used was CSVHelper, which is a C# tool with built-in CSV libraries.



### **3.3: Agent**

The second phase of simulation development involved the development of an agent class which could traverse the nest with the assigned nest-building heuristic. The agent is placed on a random location on the nest structure and will decide the best candidate building site based on “local” or “global” knowledge. In local scope, the agent walks on the nest and looks for local stimuli. In global knowledge, the agent assesses all nest locations without the need for traversal. The agent will make decisions based on the rule it has been provided. Other features of our agent model are that it can “build” or “lengthen” a cell based on whether we have enabled the three-dimensional option. The agent model is needed for the Markov chain of development.

### **3.4: Heuristics**

After the modeling of the wasp agent, nest-building heuristics were developed with initial considerations focusing on rules proposed in Karsai and Penzes (2000). The first set of rules was comprised of the following: TwoWall, MaxW, SumAMax, Random, MinAy, MinAo, MaxAy and MaxAo (Figure 1). The random rule is equivalent to picking a cell initiation site at random. The TwoWall rule picks sites with two or more adjacent walls, while the MaxW rule picks sites with the maximum number of walls. SumAMax picks the candidate with the highest summed age of neighboring cells. The “min” and “max” rules are designed to select a site that neighbors the oldest or youngest cell and the oldest or youngest neighbor of that cell.

Upon the completion of a rule, the wasp agent was assigned to start building based on the rule, and results were stored in a CSV file. The CSV information was reviewed to ensure that as the nest was built up by the agent the results were consistent

with the rule parameters. Since all rules were inherited from a single rule class, the process of implementation became developing the rule algorithms. The needed access and manipulation of nests and cells were provided in the first phase of model development.

Heuristic	Description
MaxW	Initiate cell at site with highest number of adjacent walls
SumAMax	Initiate cell at site with highest summed age of adjacent cells
SumAMin	Initiate cell at site with lowest summed age of adjacent cells
MaxAyRule	Initiate cell at site next to oldest cell and its youngest neighbor
MinAyRule	Initiate cell at site next to youngest cell next to its youngest neighbor
MaxAoRule	Initiate cell at site next to oldest cell and its oldest neighbor
MinAoRule	Initiate cell at site next to youngest cell next to its oldest neighbor

*Figure 1: Rules description based on Karsai and Penzes (2000)*

### **3.4: Markov chain**

To collect the information needed for this experiment, it was necessary that all nest permutations were captured that could occur for a given rule up to a predefined upper limit. This was achieved through a Markov model that was configurable for nest-building rules and the nest size upper limit. Once these settings had been applied, the model could be executed, and it recursively generated all nest permutations and stored them in a collection, and in a set that is filtered for compactness; the nest set is stored in a CSV file with other pertinent data, such as the number of unique nests for each size iteration N of the nest.

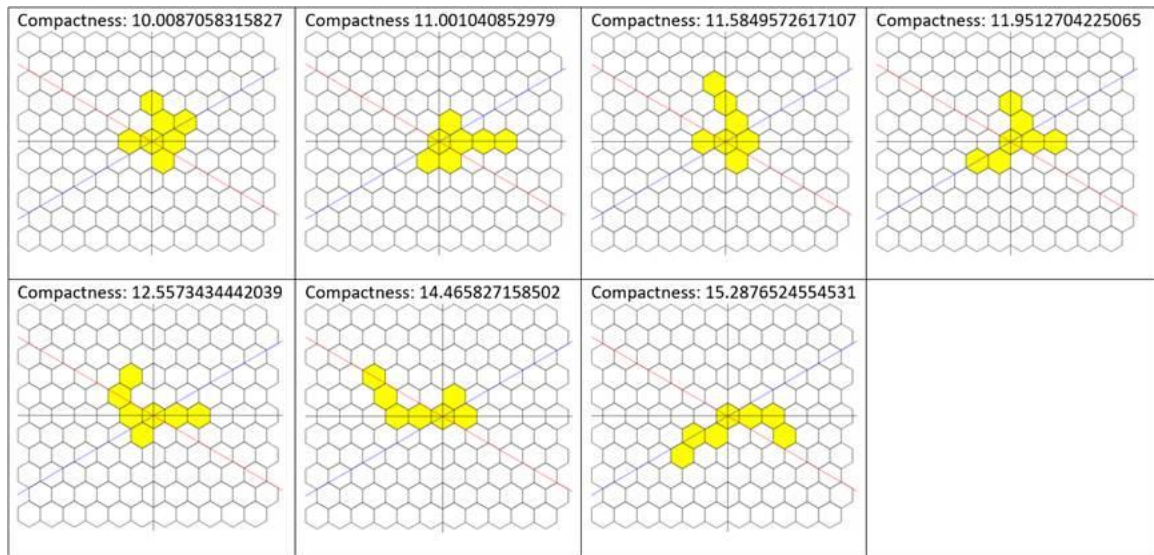
### **3.5: Data collection**

The data collection was split into several different tasks. The first of these involved the use of our nest brute force algorithm; this algorithm saved the total number of nest forms at each nest size  $N$  to a CSV file. This data was captured up to an  $N$  size of seven and compared the data to that of prior studies on compactness, Karsai and Penzes (2000) and Harrison (2018). The second task involved the Markov chain to gather rule data. For each rule, the Markov chain generated all the forms up to a maximum size of fifteen. This selected upper limit is consistent in the scope collected for Karsai and Penzes (2000). Table 1 in Karsai and Penzes (2000) included the nest sizes expected for each rule, allowing for this comparison. The third task involved the novel approach of surpassing fifteen cells to learn more about these rules and their efficacy at larger nest sizes. To do this required a simple change in the model configuration to halt the construction of the nest at a larger nest size upper limit.

## CHAPTER IV: RESULTS

### 4.1: Compactness review

The brute force algorithm was executed up to a size of seven cells. The number of unique forms for each size of N was compared to prior data. Seven extra forms were discovered at an N value of seven (331 forms compared to 324 forms); however, upon subsequent visual analysis these forms were due to a rounding error and could be safely discarded. These extraneous forms are shown in Figure 1.

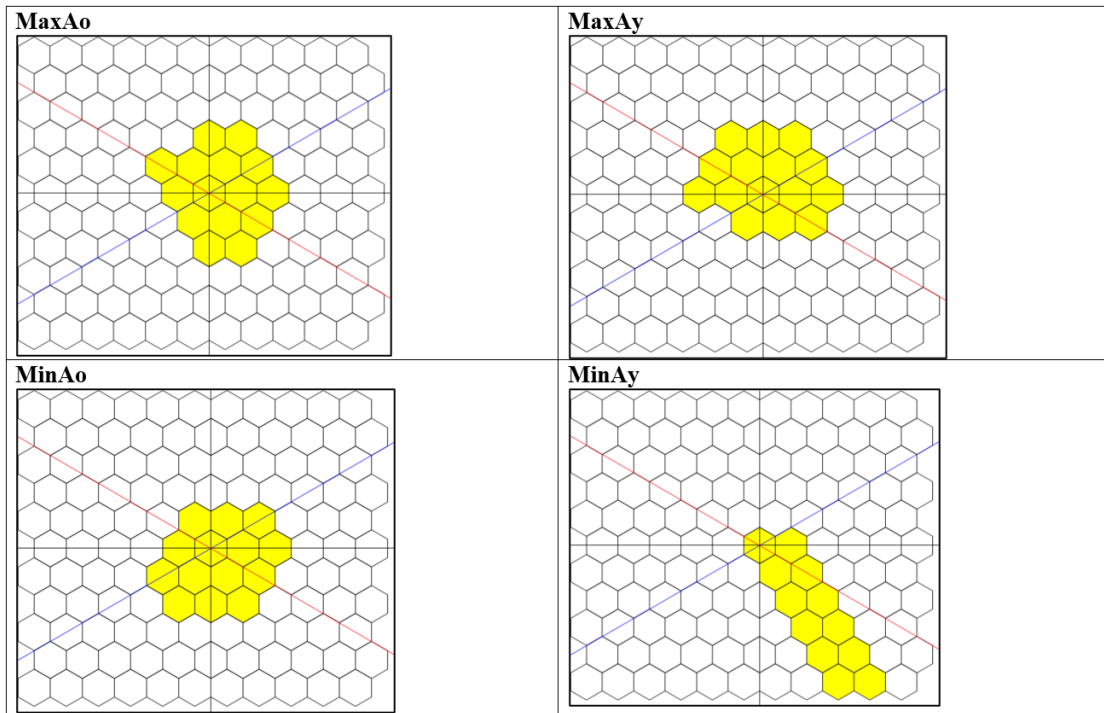


*Figure 2: Seven additional forms were found in the simulation at a nest size of seven cells. These forms were discarded due to being duplicates.*

### 4.2: Comparing algorithms with natural data

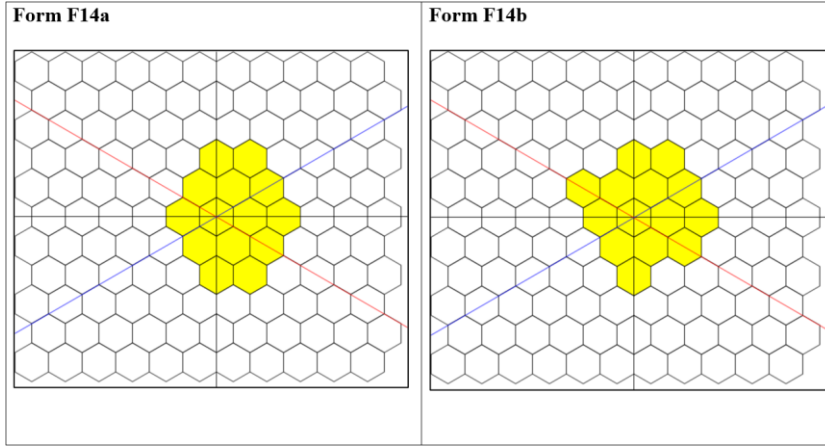
The Markov chain produced all bifurcations for the nest up to a size of fifteen and compared to Karsai and Penzes (2000). The proposed heuristics (Figure 1) were configured as the building algorithm in the Markov chain. The results have been entered into a two-dimensional visualization tool to show the kinds of rules the nest produces at fifteen cell and one-hundred cell nests.

The Markov simulation generated nests for MaxAo, MaxAy, MinAo, and MinAy. MaxAo (Figure 4). MaxAy and MinAo had no bifurcations up to fifteen cells and generated a roughly symmetric nest. (Appendix A) MinAy, however, produced an elongated nest with no resemblance to natural forms for the species of study, *Polistes dominulus*; however, there is at one least species that has exhibited this behavior. These results are consistent with prior work (Karsai and Penzes 2000).



*Figure 3: The fifteen cell nests produced by the following rules: MaxAo, MaxAy, MinAo, and MinAy.*

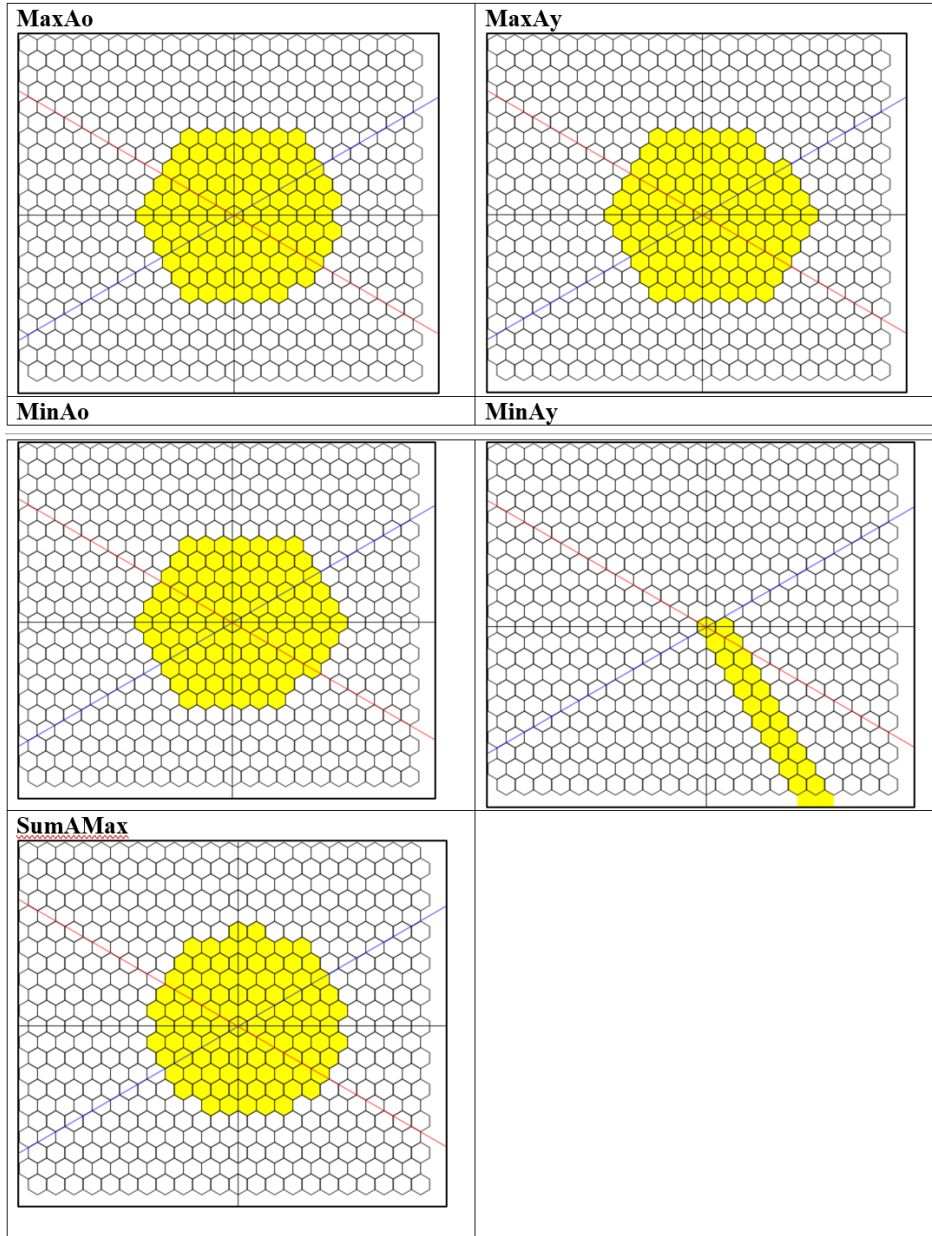
In the building rule SumAMax, the expected bifurcations were found at F6, F7, F9 and F10. The simulation discovered a bifurcation at F14 that is not reflected in Karsai and Penzes (2000). F14a and F14b were compared for their shape and compactness score and were found to be unique nests (Figure 2). The side-by-side comparison shows that form F14b is a less optimally compact shape.



*Figure 4: An additional bifurcation was discovered in the simulation at F14 for the SumAMax rule.*

### 4.3: Markov simulation at larger numbers

The simulation ran the nests at size of one-hundred cells on select rules that could compute on modern hardware with such large sizes. MaxAo, MaxAy, and MinAo produced highly symmetrical shapes even at larger numbers, while MinAy produced an elongated shape. (Figure 3) There were no bifurcations found in these rules even at this larger nest size. (Appendix 2) The rules MaxAo, MaxAy, and MinAo follow a spiral pattern that rotates around the edge of the nest.



*Figure 5: The one-hundred cell nests produced by the following rules: MaxAo, MaxAy, MinAo, MinAy, and SumAmax.*

SumAmax produced a nest that was highly symmetrical. It produced seven bifurcations at a nest size of one-hundred cells, with the number of bifurcations alternating between one and two until the nest reached the thirty-cell milestone, after

which the bifurcations started to increase at larger numbers. The simulation produced a total of 473 bifurcations for SumAMax at one-hundred cells. (Appendix 2)



## CHAPTER V: DISCUSSION

### 5.1: Compactness

The findings raise questions about compactness' efficacy. Compactness as a metric has limitations, especially at larger nest sizes, in distinguishing between unique nests. The precision of compactness is limited due to the floating-point arithmetic that must occur before the final value is derived. Due to rounding error, false positives can occur that result in duplicate nests.

There are various solutions for resolving compactness imprecision. One solution is that compactness is measured along with one or more other metrics such as number of cells, number of walls, or eccentricity. Two nests that have different compactness scores might be the same nest rotated in space, and these metrics could help verify they are non-unique. Alternatively, new research could be done to find a compactness equation that does not require floating-point operations; however, there has been no proven method to remain in integer representation.

### 5.2: Heuristics

The larger nest simulation shows that MaxAo, MaxAy, and MinAo rules never bifurcate even at larger numbers and tend to produce roughly symmetrical nests. As Karsai and Penzes (2000) showed, the MinAy rule produces an elongated shape that is unrealistic for this species of wasp and can be discarded as a realistic building heuristic. The SumAMax rule, which produced mostly optimal shapes at lower nest sizes, has proven to be less accurate than anticipated. The additional form discovered in this research, F14b, is an unnatural form and reduces the rule's accuracy; however, it cannot be ruled that the form could occur in nature but has never been observed. When

SumAMax produces a nest at one hundred cells, the nests it produces are non-optimal but still similar in compactness to the other rules besides MinAy. It can be derived from this data, therefore, that these heuristics are limited in their compactness.

Another insight from these larger nests is the unrealistic assumption that the wasp has global knowledge of the nest. These large nests have too many cells for the wasp to know which

### **5.3: Further research**

More research is needed in developing a fast and reliable method to determine unique nests. Compactness has been the preferred method to distinguish nests and has evolved with subsequent research (Harrison, 2018), but limitations remain in accuracy with nests that exceed six cells based on this research. A combination of metrics could distinguish between nests that compactness determines are separate.

Wasp heuristics have similar limitations in their ability to predict natural nest forms, especially as the nest grows. New rules should be proposed and developed with higher predictive power. Other considerations, such as wall height and nest geometry, have been abstracted for this simulation but should be included to investigate these rules further.

## APPENDIX A: NEST BIFURCATION COUNT AT FIFTEEN CELLS

The rules MaxAo, MaxAy, MinAo, and MinAy produced no bifurcations in the Markov simulation when simulated up to fifteen cells.

### *MaxAo:*

Cells	Total nests
2	2
3	3
4	4
5	5
6	6
7	7
8	8
9	9
10	10
11	11
12	12
13	13
14	14
15	15

### *MaxAy:*

Cells	Total nests
2	2
3	3
4	4
5	5
6	6
7	7
8	8
9	9
10	10
11	11
12	12
13	13
14	14
15	15

### *MinAo:*

Cells	Total nests
2	2

3	3
4	4
5	5
6	6
7	7
8	8
9	9
10	10
11	11
12	12
13	13
14	14
15	15

***MinAy:***

Cells	Total nests
2	2
3	3
4	4
5	5
6	6
7	7
8	8
9	9
10	10
11	11
12	12
13	13
14	14
15	15

The SumAMax rule produced nineteen bifurcations in the Markov simulation

when simulated up to fifteen cells.

***SumAMax:***

Cells	Total nests
2	2
3	3
4	4
5	5
6	7
7	9
8	10

9	11
10	13
11	14
12	15
13	16
14	18
15	19

## APPENDIX B: NEST BIFURCATION COUNT AT ONE-HUNDRED CELLS

The rules MaxAo, MaxAy, MinAo, and MinAy produced no bifurcations in the Markov simulation when simulated up to one-hundred cells.

### *MaxAo:*

Cells	Total nests
2	2
3	3
4	4
...	...
98	98
99	99
100	100

### *MaxAy:*

Cells	Total nests
2	2
3	3
4	4
...	...
98	98
99	99
100	100

### *MinAo:*

Cells	Total nests
2	2
3	3
4	4
...	...
98	98
99	99
100	100

### *MinAy:*

Cells	Total nests
2	2
3	3
4	4
...	...
98	98

99	99
100	100

The SumAMax rule produced 473 bifurcations in the Markov simulation when simulated up to fifteen cells.

Cells	Total nests
2	2
3	3
4	4
5	5
6	7
7	9
8	10
9	11
10	13
11	14
12	15
13	16
14	18
15	19
16	21
17	22
18	24
19	27
20	29
21	31
22	32
23	34
24	35
25	37
25	39
27	40
28	42
29	44
30	45
31	48
32	51
33	53
34	57
35	60
36	62
37	64
38	69

39	73
40	77
41	79
42	82
43	84
44	87
45	88
46	92
47	97
48	101
49	103
50	107
51	112
52	114
53	115
54	120
55	126
56	132
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94	401
95	408
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97	429
98	446
99	458
100	473

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