Population Control: An Agent-Based Approach

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INTRODUCTION

Invasive species have become a problem for both the scientific community and the general public. Ecologically speaking, invasive exotics have been found to reduce biodiversity, a commonly known indicator of ecosystem health (McGeoch *et al.* 2010). They also have the potential to alter the physical properties of an ecosystem, everything from the biogeochemistry (Gordon 1998) to soil horizon layers (Bohlen *et al.* 2004) to species composition (DiTomaso 2000).

From an economic standpoint, invasive species are generally detrimental. Pimental *et al.* estimated that in 2005 invasive species were responsible for 120 billion dollars worth of damages (2005). These can take a plethora of forms. DiTomaso reported decreased hunting and game recreation opportunities due to conversions of plant populations affecting local herbivore levels (2000). Johnson grass, an invasive plant originally brought to the United States as a forage crop, has been known to supplant and overcome entire sugarcane harvests in the state of Louisiana. Currently a collection of dead zebra mussels is blocking two thirds of a Lake Erie intake pipe that supplies water to Buffalo, NY (Cabreza and Phillips 2010). The Army Corps of Engineers estimates that it will cost between 400 and 600 thousand dollars to remove (2010).

The invasive insect Asian citrus psyllid (*Diaphorina citrii*) was recently introduced and has begun spreading in the United States. It was first found in Florida and Texas (1998 and 2001 respectively) (Grafton-Cardwell *et al.* 2006) and reports indicate that the insect has migrated into California (Fenichel 2010). Asian citrus psyllid primarily affects citrus via secretion of a honeydew that can induce mold growth (Grafton-Cardwell *et al.* 2006), stunting terminal plant growth and causing the malformation of leaf/shoot formation (Michaud 2004), and acting as a vector for the spread of citrus greening disease. Citrus greening disease or Huanglongbing is known as the most severe disease affecting the citrus family: it causes twig/limb dieback, underdeveloped fruit, and eventual tree death (Polek emphet al. 2007). As of now there is no known cure.

ACP has the potential to devastate the California citrus industry. For my Masters in Biology at Arizona State University I will be working with Eli Fenichel and Tim Warner to model optimal control policy for Asian citrus psyllid. We hope to incorporate the ecological dispersal aspect of this problem as well as the economic and social dynamic of management by farmers.

With my weaker background in Economics, I decided to begin by focusing on an ecological approach, specifically looking at dispersal models of populations. I hoped to take a basic dispersal model and expand it to investigate the effectiveness of various pest control methods on agent populations.

Several agent or individual-based dispersal models can be found in the ecological literature. Schmolke used an agent-based model to link foraging efficiency to the evolution of polydomy (multiple nests) in ants (2009). Holt *et al.* (2004) investigated how the 'Allee effect' due to immigration affected species adaptation. Further, a study conducted in 2008 utilized an individual-based model to predict the spread of the invasive velvet tree in Australia (Murphy *et al.* 2008).

For my study, I selected one by Poethke *et al.* (2003) to use a basis for my own model: it was relevant and possessed components that I felt most able to expand to fit my questions. In it the authors looked at the evolution of optimal dispersal rates for local extinction factors (environmental catastrophes and demographic fluctuations). I replicated the environmental catastrophe portion of the model, then added an age structure and modified the catastrophe component into a pest control methodology.

Model in hand, I investigated the effects of two different pest control regiments on agent populations: a time interval and a population threshold interval. I also looked at optimal combinations of the type and amount of pest control management. Realistically complete extermination may not always be the best policy.

Dispersal rates can be measured in the model. Agents will evolve an optimal dispersal rate for a given pest control method. However, the primary focus was on the aggregate population levels of agents.

MODEL DESCRIPTION

The model environment consists of 180 patches each with a patch-specific carrying capacity and agent density. Agents possess their own age, sex, patch affiliation, and four genes on two loci coding for dispersal probability.

At each time step, agents are subjected to a management control (if applicable), disperse, and reproduce. Dispersal is determined both by the agents genetic code (establishing a tolerance for other agents) and the density of agents on that agents patch. If an agent does choose to disperse, there is an equal probability of going to every patch on the environment and as well as a global dispersal mortality probability. Only adults may move to another patch.

When two adult unpaired agents of the opposite sex come together on a patch, they can mate and produce offspring. The number of offspring is drawn from a Poisson distribution with a user-defined mean, but is limited by the carrying capacity of a patch. Generally offspring inherit their parents genes for determining dispersal probability, although mutations can occur. Like dispersal, offspring are subject to a density-dependent offspring mortality rate.

For any given management control, a random patch is selected from the environment and within a user-defined block of patches all agents die. This can occur via a time interval or agent threshold. For a time interval, the control will happen after every set number of ticks defined by the user. An agent threshold approach implements a control after the total number of agents exceeds a particular amount.

A full detailed model description can be found in *Appendix A: ODD Protocol*.

RESULTS

Each management control method was conducted with an initial number of agents =300, average offspring = 10, dispersal mortality = 0.10, mutation rate = 0.10, and control intensity = 15 patches. Trials ran for 1000 time steps. Standardization determined that 150 runs per control combination was sufficient to minimize variation and give a reasonable average (0.1 percent variation). For full listings of data including standard deviations, see *Appendix B: Management Control Raw Data*.

Without any kind of external control on their populations, agent populations stabilize at about 10,250 with a dispersal rate of 0.85 (Table 1). Implementing a time control regiment did not seem to cause a significant change in agent numbers in all categories (Table 2).

Table 1 Baseline end population (no management control) with initial agents = 300, average offspring = 10, dispersal mortality = 0.10, and mutation rate = 0.10. *Avg.* and *Disp.* denote *Average* and *Dispersal* respectively.

Avg. Turtles	Median	Max	Min	Avg. Disp. Rate
10,259.86	10,325.33	12,191.60	747.01	0.85

Table 2 Time control populations with initial agents = 300, average offspring = 10, dispersal mortality = 0.10, mutation rate = 0.10, and control intensity = 15 patches. *Avg.*, *Disp.*, and *Nmbr.* denote *Average*, *Dispersal*, and *Number* respectively.With the exception of the number of controls, values are the percent change (+/-) from the baseline (null) with no control.

Interval (Ticks)	Avg. Turtles	Median	Max	Min	Avg. Disp. Rate	Nmbr. Controls
10	-1.23	-0.68	-2.68	0.41	0.70	99
20	-0.63	-0.29	-0.02	-1.74	-0.60	49
30	-0.36	-0.10	0.28	-1.71	0.74	33
40	-0.23	-0.06	-0.03	-1.56	-0.11	24
50	-0.24	-0.10	-0.04	-0.35	0.50	19
60	-0.34	-0.20	-0.39	-0.43	-0.71	16
70	-0.21	-0.11	-0.23	-0.29	-0.50	14
80	-0.08	0.04	-0.15	-1.86	-0.28	12
90	-0.03	0.06	0.22	-1.46	0.82	11
100	0.07	0.14	0.32	0.02	0.15	9
150	-0.02	0.03	-0.03	-0.82	-0.19	6
200	0.14	0.17	-0.31	-0.20	0.36	4
250	0.06	0.09	-0.14	-0.72	0.17	3
300	0.06	0.09	0.17	-1.35	-0.04	3
400	0.03	-0.26	-0.21	-1.49	-0.06	2
500	0.07	0.07	0.11	-0.25	-0.13	1

Although these changes may be statistically significant, they are not biologically significant. This most likely stems from the time lag between management controls and the agents' speed of recovery. With an average offspring of ten, agents are able to quickly recover and the control method has little effect even at the smallest time interval. Thus, in order to sufficiently suppress agent populations one would need to either increase the intensity of the control or decrease the control interval.

Pest threshold was able to cause substantial decreases in agent populations, specifically in the average and median number of turtles (Table 3). Note that this does come at the cost of the number of management controls required. Most of the pest thresholds implemented almost 100 times more controls than the latter management method.

Table 3 Pest threshold populations with initial agents = 300, average offspring = 10, dispersal mortality = 0.10, mutation rate = 0.10, and control intensity = 15 patches. *Avg.*, *Disp.*, and *Nmbr.* denote *Average*, *Dispersal*, and *Number* respectively. With the exception of the number of controls, values are the percent change (+/-) from the baseline (null) with no control.

Threshold	Avg. Turtles	Median	Max	Min	Avg. Disp. Rate	Nmbr. Controls
1000	-11.57	-11.48	-5.86	0.14	1.39	997
2000	-11.38	-11.38	-5.68	-1.70	1.38	994
3000	-11.41	-11.44	-6.01	-1.44	1.21	993
3500	-11.40	-11.43	6.00	-1.09	1.07	992
4000	-11.41	-11.45	-5.74	-1.52	1.16	992
4500	-11.32	-11.35	-5.78	-1.29	1.75	992
5000	-11.42	-11.43	-5.75	-2.06	1.37	992
5500	-11.36	-11.41	-5.85	-1.82	1.20	991
6000	-11.29	-11.33	-5.33	-0.92	1.86	991
6500	-11.38	-11.44	-5.57	-0.09	1.14	990
7000	-11.30	-11.33	-5.02	-1.13	1.52	986
7500	-10.94	-10.98	-5.01	-1.20	1.38	971
8000	-10.52	-10.56	-4.52	-1.63	0.69	921
8500	-9.26	-9.32	-4.04	-1.06	1.62	839
9000	-7.74	-7.92	-3.78	-0.74	1.39	724
9500	-6.05	-6.46	-2.54	-0.77	1.25	576
10000	-3.97	-4.32	-1.79	-0.70	1.06	402
10500	-1.61	-1.24	-1.32	-0.15	0.80	171
11000	0.08	0.16	-0.82	-2.08	0.27	14
12000	0.05	0.08	-0.10	-1.43	-0.10	1

The optimal management control for agent number threshold would be either 8500, 9000, or 9500 agents depending on the particular type of pest and cost of control. Each threshold lowers agent populations by greater than five percent and experiences a drop in the number of controls from the previous threshold level.

In order to make an educated decision one would have to weigh the effects of an agent population on the environment as well as the cost of controlling agent populations. Allowing large numbers of agents to exist may not necessarily be detrimental to an environment if that population is below a level that causes severe damage. Similarly if the cost of control is low enough one will not be penalized enough to discourage frequent management control of agent populations.

SENSITIVITY ANALYSIS

Analyses of parameter values were conducted using a pest threshold control of 9000 agents with all other variables held the same as the previous experiment. Due to time constraints trials were run 50 times instead of 150. There was still little variation (less than five percent). For full listings of data including standard deviations, see *Appendix C: Sensitivity Analysis Raw Data*

Altering dispersal probability should affect overall agent population numbers. One would expect a negative correlation between the two: as dispersal mortality increases, agents will be less inclined to disperse due to the risk of death. At high management control intensities and frequencies, there is a greater chance that agents will be caught in a control implementation compared to an agent that constantly moves around the environment.

Decreasing dispersal mortality exhibits a positive change from the baseline, while increasing it leads to a significant decrease in all turtle values as predicted (Table 4). Note the large drop in dispersal rate. At mortalities greater than 0.25 turtles were not able to survive until the end of the run and were not included. Even at dispersal mortality = 0.25, only 19 trials out of 50 produced turtles by the end of the run.

Table 4 Effect of dispersal mortality with initial agents = 300, average offspring = 10, mutation rate = 0.10, pest threshold = 9000, and control intensity = 15 patches. *Avg.*, *Disp.*, and *Nmbr.* denote *Average*, *Dispersal*, and *Number* respectively. Values are the percent change (+/-) from the baseline (dispersal mortality = 0.10). In runs with dispersal probability greater than 0.25, populations were unable to survive and were not included.

Disp. Mortality	Avg. Turtles	Median	Max	Min	Avg. Disp. Rate	Nmbr. Controls
0	5.22	5.28	8.48	16.98	0.40	17.55
0.10	0.00	0.00	0.00	0.00	0.00	0.00
0.15	-2.86	-2.88	-4.61	-7.92	-4.37	-15.14
0.2	-5.68	-5.60	-8.72	-15.50	-44.90	-34.99
0.25	-8.24	-7.43	-13.69	-16.43	-61.43	-59.26

Mutation rates have the potential to affect the effectiveness of a control implementation. If mutations lead to the development of high dispersal rates, then agents will be better at avoiding a control. For the most part shifting mutation rates had little or no deviation from the baseline measurement (Table 5). Only no mutations, that is a uniform agent dispersal probability equal to initial values, caused a difference in dispersal rate.

Table 5 Effect of mutation rate with initial agents = 300, average offspring = 10, dispersal probability = 0.10, pest threshold = 9000, and control intensity = 15 patches. *Avg.*, *Disp.*, and *Nmbr.* denote *Average*, *Dispersal*, and *Number* respectively. Values are the percent change (+/-) from the baseline (mutation rate = 0.10).

Mutation Rate	Avg. Turtles	Median	Max	Min	Avg. Disp. Rate	Nmbr. Controls
0.00	0.93	0.95	1.91	0.24	-31.70	2.79
0.05	0.05	0.07	0.69	0.41	0.05	0.28
0.10	0.00	0.00	0.00	0.00	0.00	0.00
0.15	-0.15	-0.18	-0.05	-0.58	0.10	-0.84
0.20	-0.08	-0.06	0.17	-1.21	0.37	-0.15
0.25	0.05	0.02	-0.54	-0.05	-1.25	0.22
0.30	-0.06	-0.08	-0.35	-0.8	0.43	-0.15
0.35	-0.12	-0.17	-1.37	0.10	0.52	-0.80
0.40	-0.09	-0.16	-1.20	-1.33	-1.02	-0.33
0.45	-0.32	-0.33	-1.72	-0.10	-0.28	-1.80
0.50	-0.08	-0.10	-1.41	0.01	0.39	-0.57
0.75	-0.19	-0.23	-1.01	-0.61	0.39	-0.87
1.00	-0.06	-0.10	-1.29	-1.01	0.25	-0.39

Average offspring directly impacts the power of agents to recover from a management event. High reproductive rates stemming from the number of offspring allow agents to quickly repopulate despite near-extinction. With low average offspring, populations are unable to recover from a control regiment and the population crashes. When average offspring are less than nine agent populations decline and stabilize or completely die off (Table 5). Runs with average offspring less than three were not able to survive and are not listed here. Similarly many Netlogo errors occurred with average offspring less than nine and were discounted from the experiment.

As average offspring increases populations should do better up to a point. Since reproduction is limited to the carrying capacity of a patch, having a high average offspring that exceeds a carrying capacity will have no real effect. This was not observed with the given parameters (Table 5).

Table 6 Effect of average offspring with initial agents = 300, dispersal probability = 0.10, mutation rate = 0.10, pest threshold = 9000, and control intensity = 15 patches. *Avg.*, *Disp.*, and *Nmbr.* denote *Average*, *Dispersal*, and *Number* respectively. Values are the percent change (+/-) from the baseline (average offspring = 10).

Avg. Offspring	Avg. Turtles	Median	Max	Min	Avg. Disp. Rate	Nmbr. Controls
4	-96.71	-96.75	-97.22	-60.23	-91.57	-100.00
5	-96.66	-96.67	-97.30	-58.49	-98.41	-100.00
6	-94.87	-94.87	-95.58	-58.19	-94.62	-100.00
7	-77.79	-77.00	-75.10	-54.97	-70.21	-99.78
8	-65.38	-64.00	-61.57	-45.01	-55.64	-96.01
9	-32.60	-32.22	-33.41	-16.52	-19.52	-56.85
10	0.00	0.00	0.00	0.00	0.00	0.00
11	4.41	4.50	6.10	5.29	0.97	16.09
12	8.37	8.49	13.20	12.16	1.25	24.63
13	12.20	12.33	15.78	19.43	0.25	30.05
14	15.06	15.24	21.54	26.82	1.14	32.43
15	17.19	17.34	25.29	32.86	1.51	33.73

CONCLUSIONS AND EXTENSIONS

For our particular agent population, a time interval control regiment is ineffective: the current management levels allow agents too much time to recover. A pest threshold control technique is much better at maintaining low agent populations, albeit it does come at the cost of more control implementations.

Choosing an optimal control will be agent-specific and depend on the cost of control. Depending on intrinsic agent characteristics (average offspring, threat to an environment, etc.) and extrinsic environmental factors (e.g. risk of dispersal, costs of control), various control methods will be best. For instance, if agent populations are not severely detrimental to the environment or the cost of management is high, it may be more beneficial to allow higher agent populations than to focus on extermination. In our current experiment the optimal control would most likely fall between a pest control threshold of 8500 to 9500 agents.

Extensions may include making the model spatial with multiple dispersal patterns or implementing a system of payoffs. My agent of study, Asian citrus psyllid, disperses by wind, human transplantation, and density dependent immigration. Creating a system of costs and benefits to control would also provide a more realistic setting and make it easier to define an optimal control technique. One would need a systems of costs of control as well as an agent-dependent patch costs/benefits: patches yield benefits, but agents can degrade patches reducing patch payoffs.

The model allows us to begin investigation of how different control regiments may affect a particular agent population. Further experimentation and modification is required to narrow down an optimal control path. However, the current model does provide a good basis to draw insights into the effectiveness of population control methods.

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Appendix A: ODD Protocol

Purpose
The study focuses on the effects of a management control on agent population levels. Various degrees of control implementation are evaluated order to investigate the tradeoffs between the effectiveness and number of controls required to maintain low agent population levels. Further, optimal agent dispersal rates for a particular control combination can also be determined.

This model was modified from a model by Poethke *et al.* investigating the emergence of optimum dispersal rates for local extinction events (2003). Poethke observed the evolution of stable agent dispersal rates for density-independent environmental catastrophes and density-dependent environmental fluctuations in population size.

State Variables and Scales
The model involves individual and population level hierarchies for both agents and the patch environment. Individual agents are characterized by age, sex, affiliation with a patch i, and four alleles at different loci p_c (density dependent) and p_k (patch-size dependent) which contribute to dispersal probability (d). Further, once mating with a male, females may produce Λ offspring, Λ being a Poisson-distributed number with a patch and time specific mean, Λ_{mean}(t,patch). Lambda is restricted by the patch carrying capacity. The number of agents on a patch plus offspring will never be greater than that patch's carrying capacity. Offspring develop into mature individuals with a density dependent survival probability s.

All agents are universally affected by dispersal mortality (μ), an agent control mechanism, offspring mortality, and reproductive mutation rate. The mean offspring production of the population is given by *avg-offspring*.

Patches are divided into n_{patch} habitats, each with its own carrying capacity (K_i), agent population size (N_i), and population density (C_i). The average carrying capacity of all patches is $K_{mean} = 100$.

Process Overview and Scheduling
The model progresses in single time steps. For each the following processes occur in order: management control (if applicable), agent aging, agent death (age = 4), dispersal, dispersal mortality, reproduction, and offspring mortality. At each timestep, dispersal probability, offspring mortality, and patch population size fluctuate in accordance with agent death via control, age, dispersal, and reproduction. Management control is determined by the user to occur after a specific number of ticks, when agent populations exceed a set number, or a combination of the two.

Design Concepts
Emergence The model exhibits an emergent stable dispersal rate over the course of a run.

Adaptation Agents with the optimum dispersal rate for a given management control combination will survive longer and produce more offspring than non-optimum agents. As their genes dominate the gene pool, the overall population will gradually adapt to a given control mechanism.

Fitness Fitness is determined by agents surviving longer (e.g. avoiding population control) and producing more offspring. Agents having an optimum dispersal rate for the particular control technique will have a higher fitness.

Sensing Individuals are assumed to know their own age, sex, and density, and apply those values to dispersal probability, dispersal, reproduction, and offspring survival probability.

Interaction Two forms of interaction are modeled: direct interaction via male-female reproduction, and indirect through density-dependent variables (e.g. dispersal probability).

Observation Trends in population levels and dispersal rate are constantly monitored throughout the experiment, with the final dispersal rate, average, mean, median, and min/max population levels being recorded at the end of the 1,000 timestep limit.

Initialization
At initialization, each patch i is assigned a K_i taken from the uniform distribution $10 \leq K_i \leq 190$ such that $K_{mean} = 100$. Individual agents are given an age, sex, and a patch affiliation as well as allele values of p_c =1 and $p_k = 0$. Surviving offspring at each timestep are reassigned p_c and p_k values according to the mean allele values of their parents or mutation.

Simulations are run under two methods of management control:

- *Time Control* All populations face an externally determined extinction risk independent of patch population or capacity. Populations will be randomly destroyed every a give period (*control-interval*) and intensity (*control-amt*).
- *Pest Number Control* Like the time control regiment, populations are subject to random extinctions according to overall agent population numbers. Agent threshold is determined by the user via *pest-thrsh*. If population numbers exceed the threshold a predetermined control of *control-amt* patches will be implemented on the patch environment.

In both scenarios, dispersal mortality and mutation rate were set to 0.10 with an initial agent number of 300 and average offspring (*avg-offspring*) of 10. Control intensity, the number of patches affected by a control regiment (*control-amt*), was defaulted to 15.

Input

For each timestep Λ_{mean} (t,patch) is drawn from the logarithmic distribution with a user-defined mean offspring (*avg-offspring*). However, the number of individuals on a given patch plus their offspring is limited to the carrying capacity of the particular patch.

Submodels

Dispersal

At each time step, mature individuals (age two and above) disperse in proportion to their individual dispersal probabilities, d. d is determined by local patch size and density given by:

$$d = \begin{cases} 0 & \text{if } C_i \leq C_{th} \text{ or } C_i = 0 \\ 1 - \frac{1}{C_i}(p_c - \frac{p_k}{k_i}) & \text{if } C_i > C_{th} \end{cases}$$

C_i - population density in patch i
$k_i = \frac{K_i}{K_{mean}}$ - relative carrying capacity of patch i
$C_{th} = p_c$ - $\frac{p_k}{k_i}$ - patch size dependent threshold density

Dispersal is a density dependent factor. In patches with higher densities, agents will be more likely to disperse: p_c and p_k (the genetic component) combined with a low patch carrying capacity will lead to a smaller patch size dependent threshold density. Dispersal is also assumed to be global. That is, an agent has the potential to reach any patch except its own with the same probability: $\frac{1}{(numberofpatches)-1}$

Reproduction

Once a female interacts with a male, both ages two or above, it is able to produce ε offspring. Each offspring is assigned an age of zero and p_c and p_k values that are the mean allele values of the parents. However, there is a probability of mutation, leading to the evolution of density and patch-size dependent dispersal strategies.

Offspring Mortality
Before offspring develop into mature adults, there is an initial density dependent probability of mortality (s) given by the equation:

$s = \frac{N_i}{K_i}$

N_i - populations size in patch i
K_i - carrying capacity in patch i

Like dispersal probability, offspring mortality is density dependent. At higher patch population sizes and lower patch carrying capacities, there is a much greater chance that an offspring will not survive.

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Appendix B: Management Control Raw Data

Table 7 Time interval control data with initial agents = 300, average offspring = 10, dispersal mortality = 0.10, mutation rate = 0.10, and control intensity = 15 patches. *Avg.*, *Disp.*, *Nmbr.*, and *SD* denote *Average*, *Dispersal*, *Number*, and *Standard Deviation* respectively. Values are the averages from 150 runs.

Interval (Ticks)	Avg Turtles	SD	Median	SD	Max	SD	Min	SD	Mean [d]	SD	Nmbr. Controls
10	10133.31	106.41	10254.99	105.25	11864.93	334.69	750.06	64.29	0.85	0.025	99
20	10195.64	102.32	10294.99	98.00	12188.63	370.81	733.99	60.57	0.84	0.023	49
30	10223.09	101.13	10315.03	99.84	12225.84	400.46	734.23	66.90	0.86	0.023	33
40	10235.91	108.16	10319.48	109.61	12188.07	377.71	735.33	58.34	0.85	0.025	24
50	10234.85	101.26	10315.03	97.70	12186.59	366.06	744.41	63.12	0.85	0.025	19
60	10225.44	107.55	10305.13	106.24	12143.94	409.91	743.77	65.16	0.84	0.026	16
70	10238.06	106.17	10313.58	106.99	12164.17	399.46	744.81	59.29	0.84	0.025	14
80	10251.83	93.99	10329.87	93.75	12173.83	402.33	733.11	63.84	0.85	0.024	12
90	10257.24	99.15	10331.64	99.32	12218.73	372.25	736.07	66.61	0.86	0.021	11
100	10266.57	89.77	10339.71	87.51	12231.15	387.09	747.16	69.48	0.85	0.018	9
150	10257.79	97.88	10328.57	98.50	12187.62	380.95	740.85	60.16	0.85	0.025	6
200	10273.97	87.33	10342.70	86.94	12154.02	353.60	745.53	57.86	0.85	0.023	4
250	10266.13	111.57	10334.32	108.07	12174.68	388.16	741.64	58.55	0.85	0.025	3
300	10266.08	98.85	10335.09	101.51	12212.29	371.18	736.92	67.46	0.85	0.023	3
400	10262.97	99.02	10298.09	100.09	12165.98	338.30	735.85	61.80	0.85	0.025	2
500	10266.61	101.38	10333.01	101.16	12204.57	360.96	745.17	59.48	0.85	0.023	1

Table 8 Pest threshold control data with initial agents = 300, average offspring = 10, dispersal mortality = 0.10, mutation rate = 0.10, and control intensity = 15 patches. *Avg.*, *Disp.*, *Nmbr.*, and *SD* denote *Average*, *Dispersal*, *Number*, and *Standard Deviation* respectively. Values are the averages between 150 runs.

Threshold	Avg Turtles	SD	Median	SD	Max	SD	Min	SD	Mean [d]	SD	Nmbr. Controls	SD
1000	9072.67	118.26	9140.31	122.59	748.08	64.41	11477.25	234.99	0.86	0.03	996.59	0.84
2000	9092.36	120.73	9150.48	124.74	734.33	60.87	11498.62	251.56	0.86	0.04	993.97	1.25
3000	9089.46	122.54	9144.16	125.96	736.29	67.87	11458.81	227.27	0.86	0.04	992.67	1.42
3500	9089.80	124.29	9145.13	124.30	738.88	57.38	11459.97	224.31	0.86	0.04	992.39	1.64
4000	9089.67	140.09	9143.51	144.03	735.67	58.09	11491.55	248.83	0.86	0.04	991.92	1.64
4500	9098.18	126.66	9153.70	131.90	737.38	63.59	11487.50	240.48	0.86	0.04	991.57	1.29
5000	9087.98	127.64	9144.92	132.78	731.65	60.04	11490.17	242.97	0.86	0.04	991.27	1.33
5500	9094.47	118.95	9146.76	121.49	733.39	61.69	11478.19	232.07	0.86	0.04	990.95	1.46
6000	9101.47	118.81	9155.81	118.74	740.14	66.79	11541.27	272.18	0.86	0.04	990.61	1.79
6500	9091.93	129.49	9143.92	131.63	747.66	63.42	11512.77	247.04	0.86	0.04	990.10	2.05
7000	9100.93	119.57	9155.59	123.00	738.55	59.98	11579.21	279.97	0.86	0.04	986.42	2.68
7500	9137.16	105.24	9191.13	109.04	738.03	64.88	11581.22	251.57	0.86	0.04	970.74	7.41
8000	9180.67	101.71	9235.40	106.00	734.86	59.12	11638.97	247.30	0.85	0.04	920.57	16.65
8500	9309.83	88.43	9362.93	89.87	739.11	69.58	11698.85	324.42	0.86	0.04	839.21	24.33
9000	9465.51	76.63	9507.45	83.35	741.49	59.71	11731.20	402.00	0.86	0.03	724.21	30.13
9500	9639.56	72.49	9657.98	82.75	741.22	68.35	11881.94	402.06	0.86	0.03	575.58	39.27
10000	9852.95	54.23	9879.72	45.05	741.81	66.45	11973.88	387.70	0.86	0.03	401.93	36.36
10500	10094.31	47.77	10196.88	48.15	745.92	65.70	12030.67	438.32	0.86	0.03	170.56	51.69
11000	10268.06	97.86	10341.35	99.98	731.47	63.87	12091.97	435.05	0.85	0.02	13.97	9.82
12000	10265.19	98.21	10333.54	96.59	736.31	67.85	12179.03	380.88	0.85	0.02	0.74	0.59

Appendix C: Sensitivity Analysis Raw Data

Table 9 Dispersal mortality analysis data with initial agents = 300, average offspring = 10, mutation rate = 0.10, pest threshold = 9000, and control intensity = 15 patches. *Avg.*, *Disp.*, *Nmbr.*, and *SD* denote *Average*, *Dispersal*, *Number*, and *Standard Deviation* respectively. At dispersal mortalities greater than 0.25 agent populations were unable to persist until the end of the run and were not included. Recall that the baseline dispersal mortality = 0.10. Values are the average of 50 runs (dispersal mortality = 0.25 consisted of only 21 runs).

Disp. Mortality	Avg Turtles	SD	Median	SD	Max	SD	Min	SD	Mean [d]	SD	Nmbr. Controls	SD
0.00	9959.16	90.65	10009.46	96.86	12725.64	402.79	867.42	74.62	0.86	0.04	851.28	21.62
0.10	9441.94	77.50	9481.82	84.55	11807.36	344.54	731.82	72.04	0.85	0.04	719.68	30.28
0.15	9194.73	70.78	9233.74	81.33	11190.26	290.67	682.78	69.19	0.82	0.22	614.54	38.34
0.2	7883.79	81.15	7921.52	64.37	9500.90	274.45	551.36	59.41	0.47	0.41	414.32	50.10
0.25	8685.96	45.57	8800.68	41.23	10125.42	177.32	619.68	51.61	0.33	0.35	295.05	53.52

Table 10 Mutation rate analysis data with initial agents = 300, average offspring = 10, dispersal mortality = 0.10, pest threshold = 9000, and control intensity = 15 patches. *Avg.*, *Disp.*, *Nmbr.*, *SD* denote *Average*, *Dispersal*, *Number*, and *Standard Deviation* respectively. Recall that the baseline mutation rate = 0.10. Values are the average of 50 runs.

Mutation Rate	Avg Turtles	SD	Median	SD	Max	SD	Min	SD	Mean [d]	SD	Nmbr. Controls	SD
0.00	9553.14	69.79	9597.48	73.62	11954.90	236.66	743.28	53.56	0.59	0.03	744.40	22.50
0.05	9469.95	77.49	9514.02	75.65	11812.16	328.65	744.56	81.73	0.86	0.04	726.20	27.42
0.10	9464.64	83.37	9504.61	88.01	11700.54	366.43	735.30	54.63	0.85	0.04	723.48	32.47
0.15	9451.65	70.97	9490.81	81.70	11724.92	289.50	737.20	73.33	0.86	0.04	718.12	30.25
0.20	9457.63	74.87	9501.45	81.34	11751.53	399.72	732.51	63.71	0.86	0.03	723.12	30.03
0.25	9470.19	98.38	9509.33	109.84	11668.28	313.50	741.12	49.81	0.85	0.04	725.80	38.01
0.30	9459.78	77.36	9499.50	86.25	11690.70	327.51	735.22	63.39	0.86	0.04	723.10	30.56
0.35	9454.61	82.11	9490.96	91.55	11571.00	227.27	742.20	55.73	0.87	0.04	718.40	32.93
0.40	9456.96	82.36	9492.33	88.65	11590.92	199.20	731.62	58.62	0.85	0.04	721.80	32.52
0.45	9435.66	76.21	9475.84	82.61	11529.20	196.74	740.72	61.65	0.86	0.03	711.20	30.70
0.50	9457.49	71.83	9498.23	73.54	11566.00	233.13	741.57	59.89	0.86	0.03	720.06	26.41
0.75	9447.26	86.20	9485.64	92.58	11612.42	287.44	737.00	59.11	0.86	0.03	717.90	36.43
1.00	9460.20	77.35	9497.54	79.51	11580.28	210.99	734.04	67.69	0.86	0.04	721.38	31.26

Table 11 Average offspring analysis data with initial agents = 300, dispersal mortality = 0.10, mutation rate = 0.10, pest threshold = 9000, and control intensity = 15 patches. *Avg.*, *Disp.*, *Nmbr.*, *SD*, and *Off.* denote *Average*, *Dispersal*, *Number*, *Standard Deviation*, and *Offspring* respectively. Recall that the baseline average offspring = 10. At average offspring levels below nine, agent populations were either unable to exist or persisted at low levels; runs with agent extinction were not included. Values at levels ten and above were averages of 50 runs.

Avg Off.	Avg Turtles	SD	Median	SD	Max	SD	Min	SD	Mean [d]	SD	Nmbr. Controls	SD
4	311.16	89.47	309.23	91.09	326.19	78.28	294.92	114.98	0.07	0.22	0.00	0.00
5	316.17	71.13	316.17	71.13	316.17	71.13	307.82	51.95	0.01	0.08	0.00	0.00
6	485.79	1225.05	488.00	1239.48	518.48	1333.66	310.02	79.11	0.05	0.18	0.00	0.00
7	2102.71	3151.29	2187.00	3312.55	2921.09	3983.54	333.91	203.78	0.26	0.37	1.63	5.36
8	3277.03	3543.23	3422.45	3716.13	4507.79	4709.81	407.73	185.75	0.38	0.40	28.88	108.65
9	6379.65	3926.78	6444.07	3937.52	7811.59	4797.10	618.97	163.05	0.69	0.29	312.47	245.46
10	9452.54	99.87	9498.31	107.53	11685.22	376.59	737.54	66.79	0.86	0.04	719.60	43.01
11	9882.92	129.53	9934.85	133.52	12446.30	477.83	780.70	63.09	0.87	0.04	840.72	33.77
12	10257.58	153.13	10314.76	158.26	13279.98	566.42	831.68	65.05	0.87	0.04	902.60	23.62
13	10620.06	154.07	10679.78	158.04	13581.82	544.07	885.56	77.95	0.86	0.03	941.80	17.43
14	10891.09	118.65	10956.08	123.47	14257.96	579.10	940.38	72.27	0.87	0.03	959.10	8.94
15	11092.94	101.83	11156.45	106.81	14698.14	593.58	985.12	78.74	0.87	0.03	968.48	5.72