

An Analysis of the Trojan Y-Chromosome Method of Invasive Species Management

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26 July 2013

Abstract

Management of invasive species towards the goal of preserving native biodiversity and preventing economic damage has traditionally been one of the most challenging problems faced by modern ecological scientists. The introduction of modified members of the invasive species, carrying extra trojan y-chromosomes, may offer a much less harmful, and thus less expensive technique for controlling or eliminating wild populations of undesired, sexually reproducing organisms. This paper presents both deterministic and Stochastic models of the reaction of the wild population to such trojan introduction. Results upon arbitrary species parameters support the potential validity of this technique, and give insight into more environmentally specific interactions.

1 Introduction

For many years, and now to an increasing extent, the issues caused by invasive species have helped cause severe losses in economic productivity. Similarly, to the extent that we as a species have decided that local biodiversity is a desirable thing, and worthy of preservation, such invasive groups pose a dire threat. Zebra mussels in American waterways, fire ants in the South of the same nation, and Australia's cane toads are only among the most visible of many such problematic species.

The impetus behind study of the *Trojan Y-Chromosome* strategy for the elimination of alien species stems from the general inefficacy of previous attempts. When one's goal is to prevent the destruction of biodiversity, poisoning the environment to eliminate the target group is not particularly helpful, causing, as it does, the concurrent elimination of the desired groups. The introduction of a natural predator or competitor could in theory work very well, but in practice has a rather dismal track record, the above example of the cane toad having been caused by just such an intentional introduction.

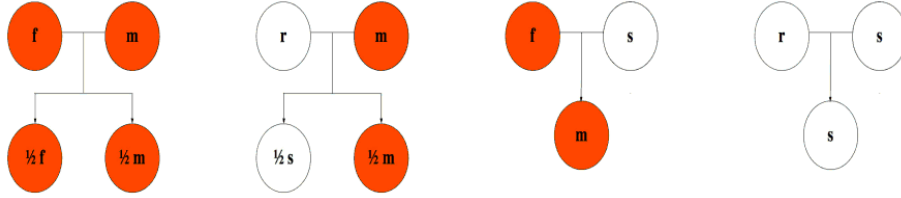


Figure 1: Pedigree tree for mating interactions among wild-type and trojan members of a species where m represents wild-type males, f is wild-type females, s denotes trojan (YY) males, and r give trojan females.

Introduction of members of an invasive species with altered chromosomes, specifically having two Y chromosomes (thus the strategy name), seeks to avoid these issues by creating a system where reproduction among the target species becomes autocidal to the group in question. This can be best seen in a mapping of breeding among the four groups in question where it can easily be seen that the only way for wild-type female offspring to arise is through one of six possible breeding outcomes.¹ The goal is thus to so alter the normal sex-ratio of individuals in the species as to drive the wild-type members to extinction.

Analysis of this theory, in combination with the above pedigree tree yields the following system of ordinary differential equations

$$\begin{aligned} \frac{df}{dt} &= \frac{1}{2}\beta fmL - \delta f \\ \frac{dm}{dt} &= \beta L(\frac{1}{2}fm + \frac{1}{2}rm + fs) - \delta m \\ \frac{ds}{dt} &= \beta L(\frac{1}{2}rm + rs) - \delta s \\ \frac{dr}{dt} &= \mu - \delta r \\ L &= 1 - \frac{f+m+s+r}{K} \end{aligned}$$

where β represents the birth rate, δ represents the death rate, L is the logistics term, K is the carrying capacity, μ is the rate of introduction of trojan specimens, here females, and the combinations of birth terms (e.g. $\frac{1}{2}rm + rs$ for trojan males) arise from the application of the mass action law to breeding patterns.

A substantial analysis of this model can be seen in the work by Xueying Wang et al. [?], but in brief, major conclusions reached show that, given the extinction of wild-type females, there are only two stable equilibria, both requiring the subsequent extinction of wild-type males, and if the introduction of trojan females (trojan males are of course produced through breeding), then only one stable equilibrium remains, that being the case where all individuals are dead.

This paper thus takes as a starting premise the assumption that stable equilibria at extinction exists for all systems concerned. The following work will then proceed to ask the the questions: how will the deterministic system behave

¹Image Citation: [?]

under a minimization of μ , how will the same be expressed under alternate models and types of trojan introduction, and how might such results change when considered from either a 0-dimensional or 2-dimensional Stochastic perspective. Possible answers will subsequently be suggested through targeted examples using arbitrary, but hopefully not unreasonable starting parameters.

2 Bang-Bang Analysis

The premise of a bang-bang system is that for some spacial interval (usually time), one state exists, and after that spacial interval, another exists. When applied to the Trojan Y-Chromosome system, the bang-bang system manifests itself as a time interval from t_0 to t_1 for which μ has some positive constant value, and after which $\mu = 0$.

We examine this system as we consider the feasibility of implementation strategies². Clearly a trojan input for all time would be impractical, so we attempt to minimize, in a bang-bang scenario, the time over which we supply the modified group. Here, we choose arbitrary parameters, though hopefully ones which correspond to reasonable expectations of reality, and define the extinction state to be $< .01K$ for carrying capacity K . We then reduce the cut of time for μ such that the wild-type females and males still reach extinction by the end of the simulation.

In this case, it should be noted that for a seemingly reasonable introduction rate, species die off in a seemingly reasonable amount of time, suggesting the potential viability of this technique as here described.

2.1 Proportional Model

The model as so far described will, of course, have many problems. One, however, stands out as potential significant, that is, the reliance on the mass action law, in that it does not take into consideration potential selective pressure on breeding behavior. We thus suggest a simple alteration to the system of equations to include variables of proportionality, that is, the relative proportions of mating pairs of individuals to represent selective pressure.

$$\begin{aligned}
 \frac{df}{dt} &= \frac{1}{2}\beta fmP_{fm}L - \delta f & P_{fm} &= \frac{fm}{(f+r)(m+s)} \\
 \frac{dm}{dt} &= \beta L(\frac{1}{2}fmP_{fm} + \frac{1}{2}rmP_{rm} + fsP_{fs}) - \delta m & P_{fs} &= \frac{fs}{(f+r)(m+s)} \\
 \frac{ds}{dt} &= \beta L(\frac{1}{2}rmP_{rm} + rsP_{rs}) - \delta s & P_{rm} &= \frac{rm}{(f+r)(m+s)} \\
 \frac{dr}{dt} &= \mu - \delta r & P_{rs} &= \frac{rs}{(f+r)(m+s)} \\
 L &= 1 - \frac{f+m+s+r}{K}
 \end{aligned}$$

Here, selective pressures are equal between modified individuals and wild-types, however disjoint versions could easily be created through the simple use of constants in front of the terms of proportionality such that the set still summed to 1.

²see Figure 2

Bang–Bang Basic Analysis (F4) for $B = 1$, $d = 0.5$, $K = 100$, $\mu = 14$

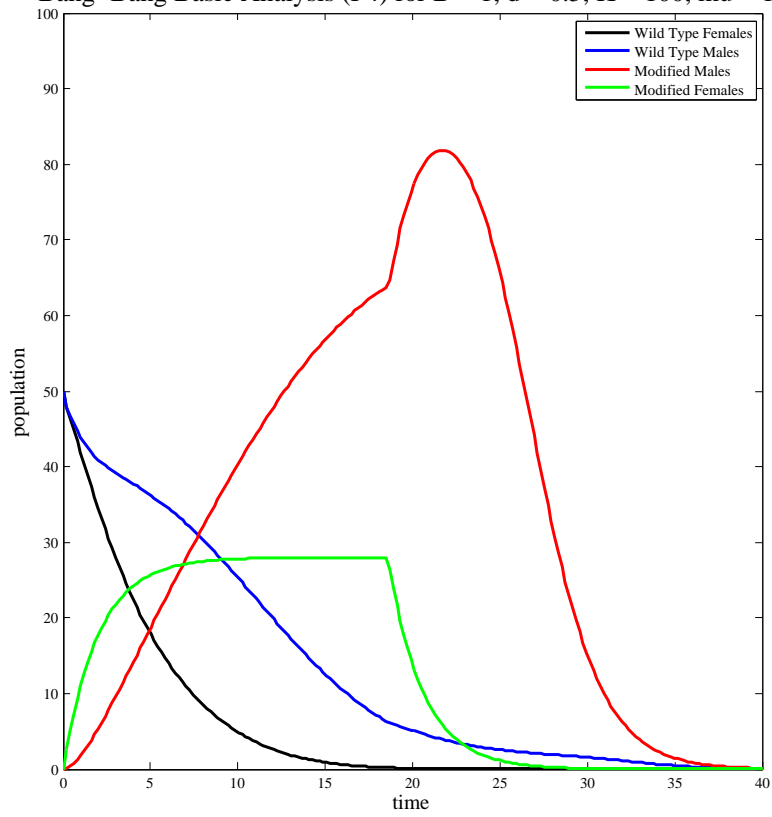


Figure 2:

Bang–Bang Proportional Analysis (F4) for $B = 1$, $d = 0.5$, $K = 100$, $\mu = 14$

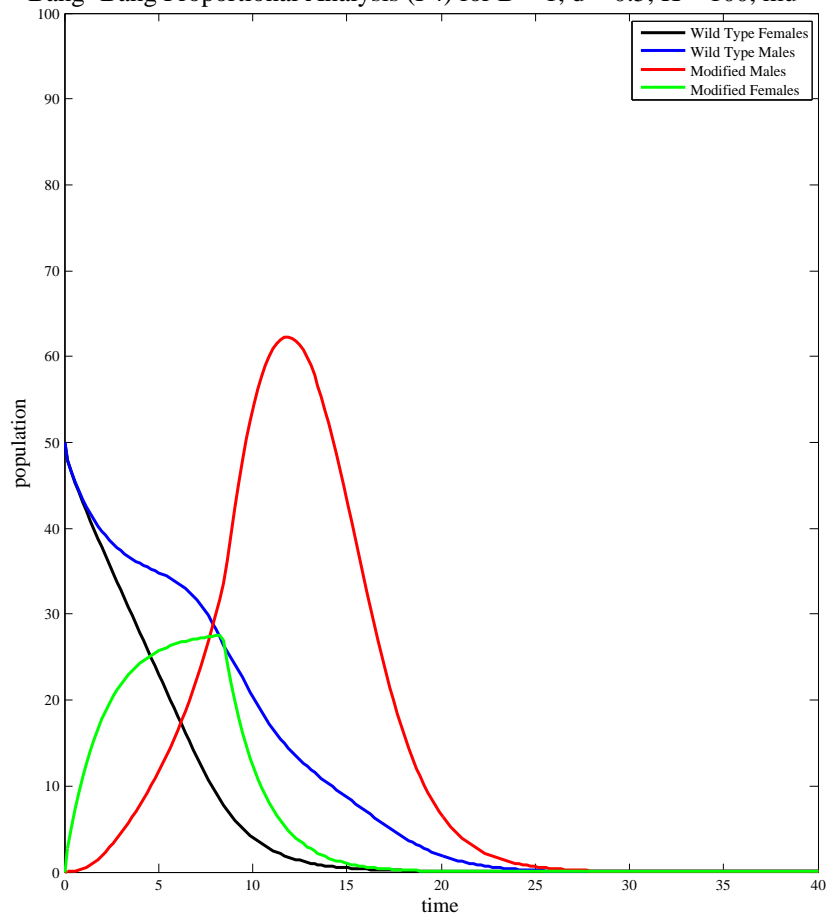


Figure 3:

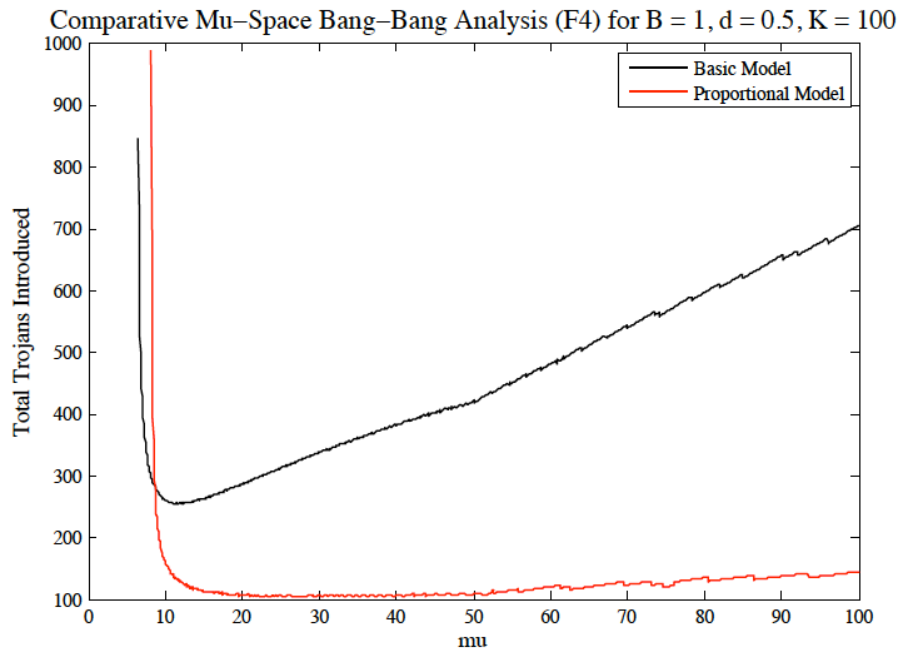


Figure 4:

One can easily see why such a model might be significant from the point of view of either the group implementing such a strategy or those breeding the trojans to be introduced. Even under this simple alteration³, the minimization of μ requires roughly half of the input that the basic, non-selective model does.

And so we must ask the question of how to look at μ minimization over various space. It would be nice to look at this question analytically, but the complexity of the problem has prevented that analysis here. However, we can give a simple spectral analysis of μ -space for our selected arbitrary parameters in the hopes that the results will give insight into the general behavior of the system.

In this figure, we see really what we would expect for the two models, basic and proportional, through μ -space in terms of the total number of trojans which would need to be supplied. On the left appears a vertical asymptote, not surprising as too low of an input rate should, as demonstrated here, merely reduce wild populations, but reach a new equilibrium short of the extinction state. As μ approaches K (here 100), the logistics term prevents further breeding events, causing population change to be defined by the death term. As this time to extinction is generally the same across all μ for which the logistics term is 0, higher μ will give the demonstrated higher cost in introduced trojans. Thus we are left with an absolute minimum in trojans introduced, comfortably sit-

³see Figure 3

uated at a seemingly reasonable percentage of K , and the previous analysis of the causes behind the shape of the graph for these parameters leads this paper to suspect that similar results would be obtained for all other combinations of parameters corresponding to reasonable biological systems.

2.2 Trojan Male Introduction

With the goal of offsetting the sex ratio, the previous pedigree tree reveals that introduction of modified females is not the only way to create a higher percentage of male offspring. Instead, one could introduce only the trojan males. This would clearly not be as effective in an absolute sense as the offspring ratio is now slightly less against female offspring. However, it turns out that current strategies for producing these trojan varieties can only produce modified females by chemically treating the aforementioned modified males in their infancy. If the mere introduction of modified males could be demonstrated to be sufficiently effective, this might represent a not insignificant savings margin at the production level. Fortunately the systems of differential equations can be easily modified:

$$\begin{aligned}\frac{df}{dt} &= \frac{1}{2}\beta fmL - \delta f \\ \frac{dm}{dt} &= \beta L(\frac{1}{2}fm + fs) - \delta m \\ \frac{ds}{dt} &= \mu - \delta s \\ L &= 1 - \frac{f+m+s}{K}\end{aligned}$$

with the corresponding proportional form:

$$\begin{aligned}\frac{df}{dt} &= \frac{1}{2}\beta fmP_mL - \delta f & P_m &= \frac{m}{(m+s)} \\ \frac{dm}{dt} &= \beta L(\frac{1}{2}fmP_m + fsP_s) - \delta m & P_s &= \frac{s}{(m+s)} \\ \frac{ds}{dt} &= \mu - \delta s \\ L &= 1 - \frac{f+m+s}{K}\end{aligned}$$

The results under a spectral sampling of μ space are as we had hoped, generally similar⁴. The curve shape matches the presumed forces acting upon it, and thus simultaneously validates our hope that such a strategy might prove effective. It now remains for relevant parties to do a cost analysis to determine their own approach.

Cost reduction, however, does in fact have us ask the question: is the breeding derived change in the sex ratio causing the elimination of the wild-type female population, or is it instead the effect of the logistics term. In effect, would a sterile introduction, with equations:

$$\begin{aligned}\frac{df}{dt} &= \frac{1}{2}\beta fmL - \delta f \\ \frac{dm}{dt} &= \beta \frac{1}{2}fmL - \delta m \\ \frac{ds}{dt} &= \mu - \delta s \\ L &= 1 - \frac{f+m+s}{K}\end{aligned}$$

⁴see Figure 5

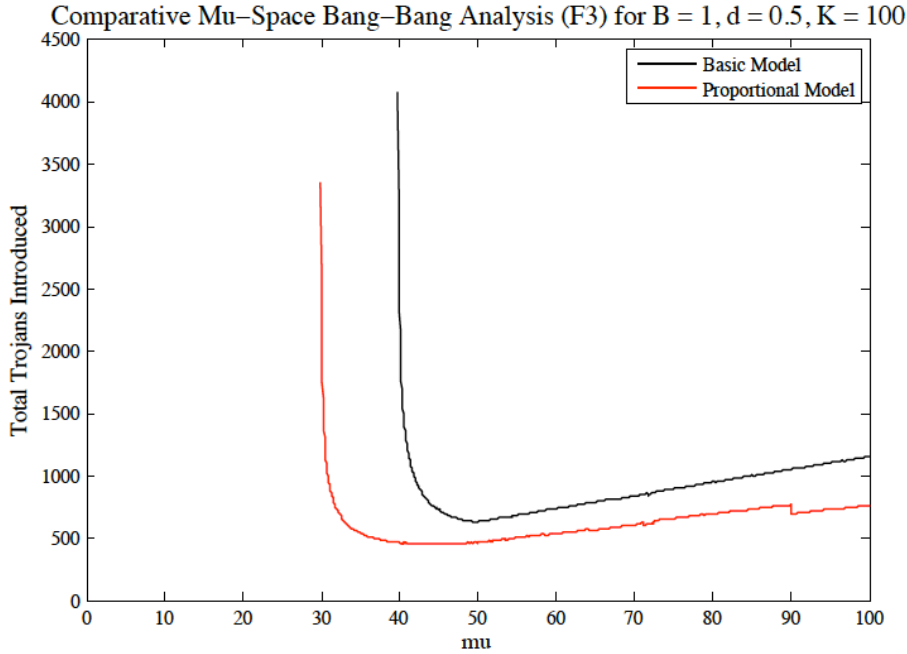


Figure 5:

where s now denotes the population of sterile individuals, prove potential effective. As shown below⁵, the answer is yes, subject, of course, to an analysis of production and implementation costs. Presumably, though, it may prove much less expensive to produce non-breeding versions of the population than genetically altered ones.

3 Stochastic Analysis

To this point, only deterministic systems have been considered. These are of course highly effective under the proper conditions, especially those of high population values where random fluctuations often manifest themselves as slight variations from mean tendencies. However, the whole point of the trojan y-chromosome introduction process is to cause extinction events. Such low population events are, of course, the realm of random occurrences.

We begin the analysis by converting the deterministic model for modified

⁵see Figure 6

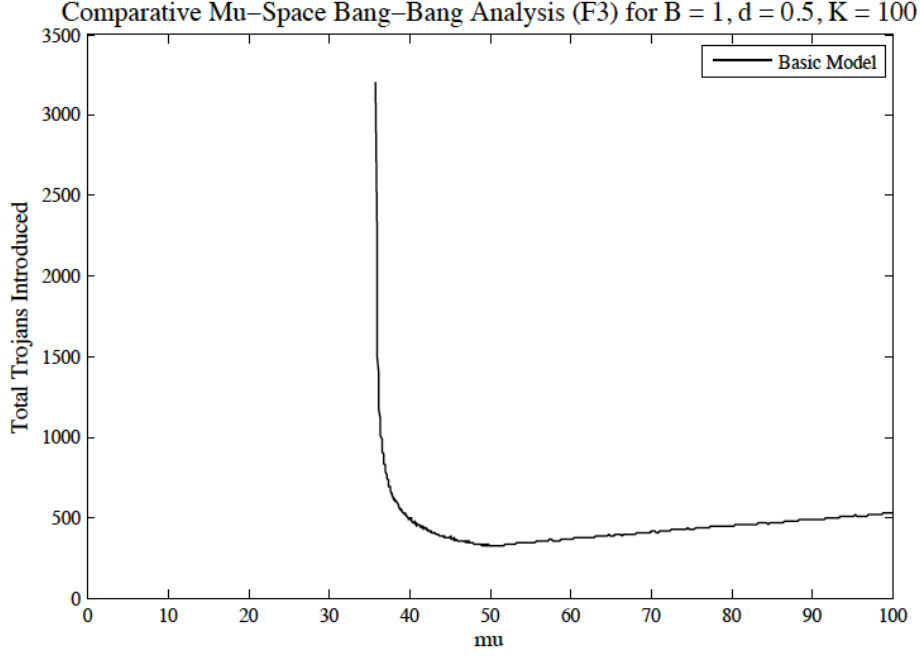


Figure 6:

female introduction into a set of eight birth and death probabilities

$$\begin{array}{ll}
 F \text{ Birth} = \frac{1}{2}\beta fm & F \text{ Death} = \frac{1}{2}\beta fmL' + f \\
 M \text{ Birth} = \beta(\frac{1}{2}fm + \frac{1}{2}rm + fs) & M \text{ Death} = \beta L'(\frac{1}{2}fm + \frac{1}{2}rm + fs) + m \\
 S \text{ Birth} = \beta(\frac{1}{2}rm + rs) & S \text{ Death} = \beta L'(\frac{1}{2}rm + rs) + s \\
 R \text{ Birth} = \mu & R \text{ Death} = r \\
 L' = \frac{f+m+s+r}{K}
 \end{array}$$

where we have non-dimensionalized in δ , meaning that β now represents the birth constant, birth rate over death rate, and time is measured in units of $t * \delta$. L' represents the negative portion of the logistics term.

The following data⁶ was produced through collating the data from 40,000 stochastic runs the same parameters as the deterministic model, and it is initially encouraging, representing, under our admittedly arbitrary parameters, a relatively quick decay extinction on the part of wild-type females where the dashed line for each of the represented populations is their mean value through time, and the vertical shading gradient gives a visual representation of the probability distribution through population space at a given time.

An examination of the probability distribution⁷ of time to extinction of wild-type females confirms this conclusion for this particular set of conditions, but

⁶see Figure 7

⁷see Figure 8

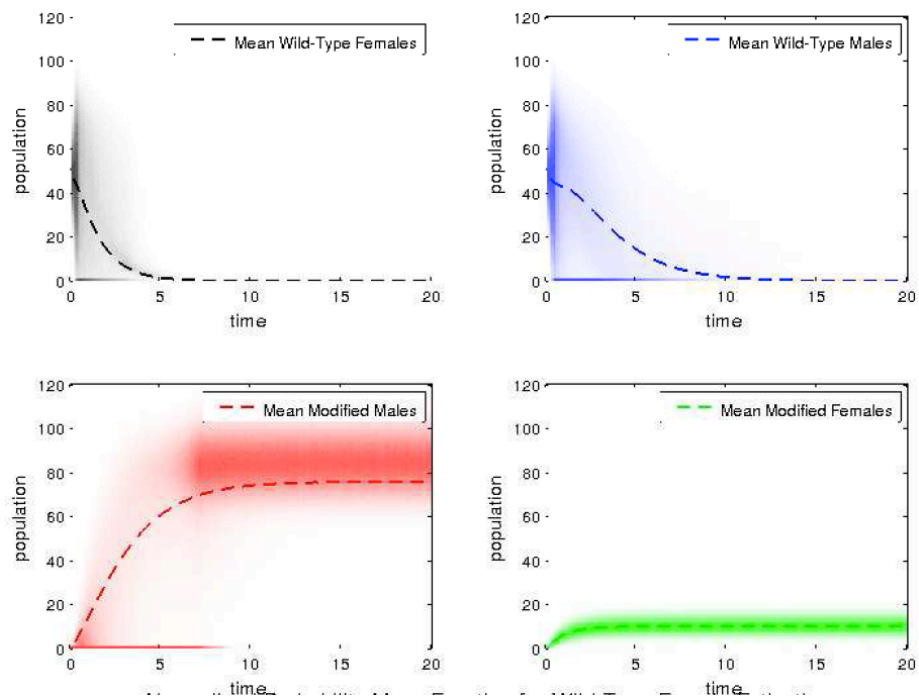


Figure 7: Spatial distribution of populations through time.

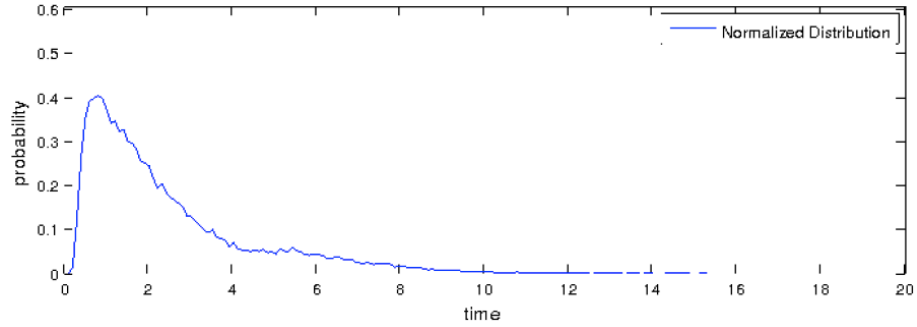


Figure 8: Probability distribution of time to extinction of the wild-type female population with $mean = 2.42$, $variance = 3.93$, and $skewness = 12.2$.

also speaks to the necessity of greater caution than the deterministic analysis gives. The distribution has quite a long, high-time-to-extinction tail, representing the not insignificant possibility that introduction time would need to be much longer than the mean would suggest.

3.1 Spatial Stochastic

Previous models, and previous analysis has limited itself to the zero-dimensional case – the proverbial well mixed pot scenario. The probabilities can be easily be modified to a spacial system with the mere introduction of a migration term.

$$\begin{aligned}
 F \text{ Birth} &= \frac{1}{2}\beta fm & F \text{ Death} &= \frac{1}{2}\beta fmL' + f \\
 M \text{ Birth} &= \beta(\frac{1}{2}fm + \frac{1}{2}rm + fs) & M \text{ Death} &= \beta L'(\frac{1}{2}fm + \frac{1}{2}rm + fs) + m \\
 S \text{ Birth} &= \beta(\frac{1}{2}rm + rs) & S \text{ Death} &= \beta L'(\frac{1}{2}rm + rs) + s \\
 R \text{ Birth} &= \mu & R \text{ Death} &= r \\
 L' &= \frac{f+m+s+r}{K}
 \end{aligned}$$

$$\text{Migrate} = \frac{\text{population} * \text{migration_speed}}{\text{cell_length}}$$

There are many ways in which to introduce the migration term, none particularly better than others except in how they relate to specific species. Here, as a general base case, we have adopted a random-walk type migration, giving a probability based on system parameters of a migration event taking place on a cell by cell basis. The probabilities of directional migration are thus the probability of a migration taking place divided by the number of viable directions to migrate too. Here we model the environment as a simple grid and limit movement to up, down, left, and right, with the particular habitat analyzed shown below⁸.

Here, the green squares represent the cells in which we input our trojan varieties. Working specially allows us to add this degree of realism to the system.

⁸see Figure 9

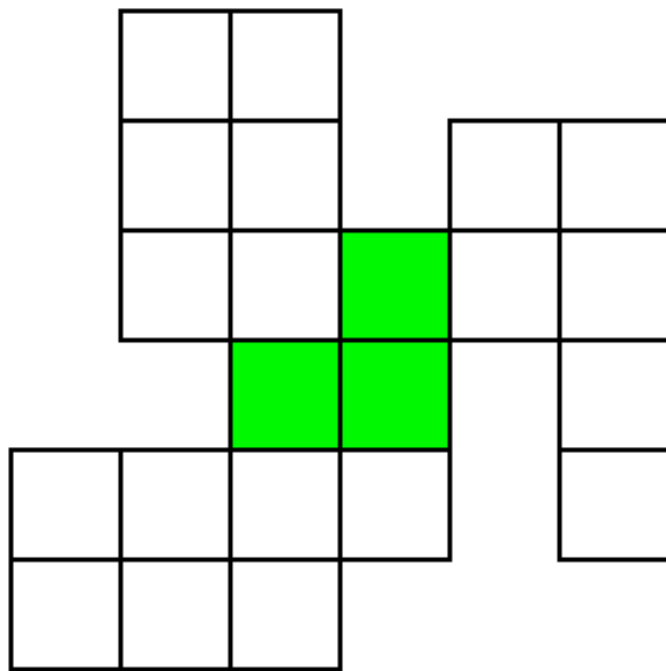


Figure 9: Sample habitat

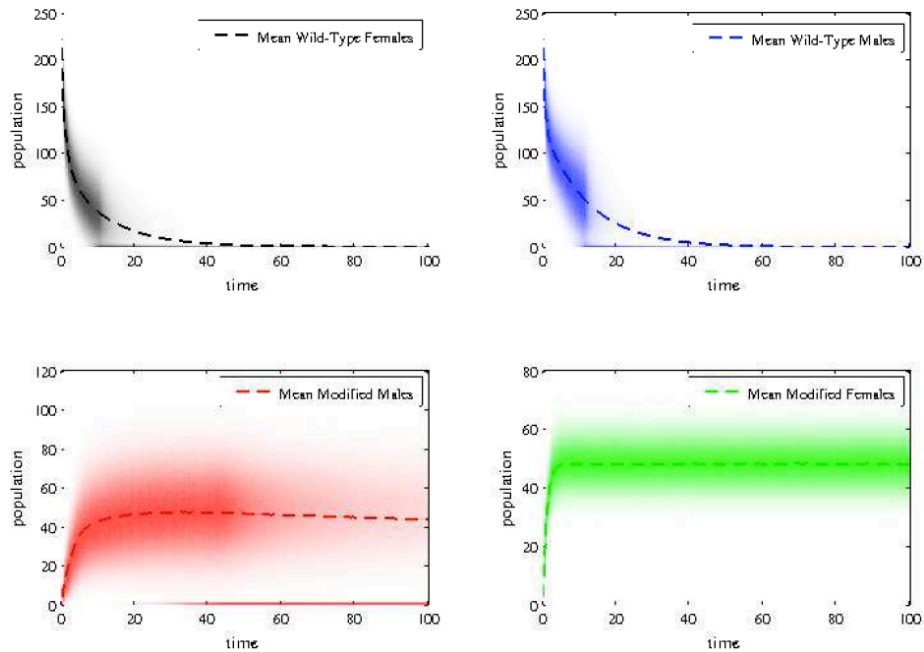


Figure 10:

In most cases of invasive species management, the population would presumably be spread over a large area, preventing uniform introduction.

The results of this run are, perhaps not surprisingly, quite similar to the previous systems⁹. Here, we have preserved the previous parameters, and given a relatively low migration rate with $migration_speed = 1$ and $cell_length = 1$.

Examining the distribution of time to extinction¹⁰, we see the same, similar results, except, of course, that we have increased our mean time to extinction – here measuring the time to zero wild-type female population through the whole system – by an order of magnitude. This should not come as much of a surprise, given that in order for the trojan populations to be able to act upon the wild populations of distant cells, they must first migrate there. However, it does highlight the question of where one might optimally introduce trojan varieties. This is further emphasized by the data right of the extinction time distribution, where cell by cell mean times to extinction are showed on a gradient scale where white is the maximum time to extinction. In fact, the locations where one might reasonably expect the shortest time to extinction, i.e. directly under the introduction locations, are in the middle of extinction times, suggesting that outside wild populations are migrating in sufficiently quickly to prevent this.

An examination of the same run under a different distribution of introduction

⁹see Figure 10

¹⁰see Figure 11

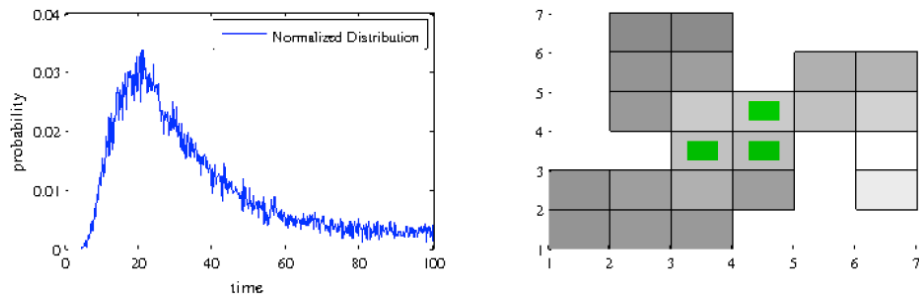


Figure 11: Probability distribution of time to extinction of the wild-type female population with $mean = 35.3$, $variance = 465$, and $skewness = 11,500$ and cell-wise mean time to extinction with $maximum_time = 27.7$

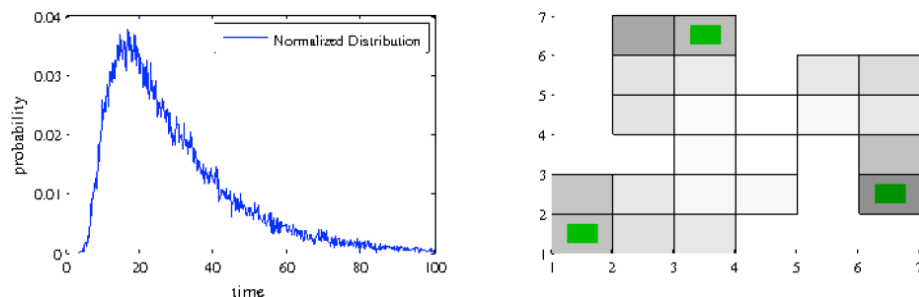


Figure 12: Probability distribution of time to extinction of the wild-type female population with $mean = 28.9$, $variance = 295$, and $skewness = 6,690$ and cell-wise mean time to extinction with $maximum_time = 26.7$

locations¹¹ demonstrates the importance of location choice. Here, with corner inputs, several units of time have been shaved off of the mean time to extinction, and both the variance and skewness of the distribution have been significantly reduced.

4 Conclusion

What we unfortunately don't have is a set of analytic analyses on these various models. However what we do is a set of powerful tools for finding answers to the relevant questions, questions of species, environment, and behavior.

More significantly, however, it seems like we have tools to point in the direction of which questions to ask. Which model is appropriate: deterministic or Stochastic; basic or proportional; trojan female introduction, trojan male introduction, or something else; 0-dimensional or spacial? In particular, it would be very interesting to see a more robust analysis of spacial geometries of intro-

¹¹see Figure 12

duction locations in the continuation of the effort to minimize the amount of trojans it is necessary to introduce. However, under the correct circumstances, this technique does appear to lend itself as one of the more viable options in invasive species control.

References

- [1] Linda J. S. Allen. *An Introduction to Stochastic Processes with Applications to Biology*. Pearson Education, 2003.
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- [3] Xueying Wang, Jay R. Walton, Rana D. Parshad, Katie Storey, and May Boggess. Analysis of the trojan y-chromosome eradication strategy for an invasive species, 2013.