ABSTRACT

Title:	REPRODUCTIVE POTENTIAL WITHIN THE LANDSCAPE: A SPATIALLY-EXPLICIT, AGENT-BASED MODEL OF ASYNCHRONY
	Christopher Roland Guenther, Master of Science, 2005
Directed By:	Professor William F. Fagan, Department of Biology

Reproductive asynchrony, which can be a beneficial life-history strategy in healthy insect populations, may contribute to an Allee effect at small population densities. A spatially explicit, agent-based model is used to investigate quantitative effects of asynchrony on reproductive potential. Temporal and spatial isolation effects are treated independently and together. Three behaviors are explored: clustered emergence from host plants, hilltopping, and mating discretion by females. The magnitude of the reduction in overall spatial overlap within the simulated population is shown to be governed by the radius of circular, random-walk movement and potential interaction distance. Hilltopping behavior and clustered emergence partially alleviate detrimental effects of spatial isolation; female selectivity in mating can exacerbate the loss of reproductive potential. Among these three behaviors, hilltopping produced the largest differential in spatial/temporal overlap.

REPRODUCTIVE POTENTIAL WITHIN THE LANDSCAPE: A SPATIALLY-EXPLICIT, AGENT-BASED MODEL OF ASYNCHRONY

By

Christopher Roland Guenther

Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Science
2005

Advisory Committee:
Professor William F. Fagan, Chair/Advisor
Professor David Levermore
Professor James Reggia

Table of Contents

List of Figures

Chapter 1: Introduction

1.1 Reproductive Asynchrony

Reproductive asynchrony is a biological condition in which the period of time any individual member of a population is reproductively active is a subset of the reproductive activity period for the population as a whole. This behavior has been found in a wide range of species. Detailed quantitative data have been collected on "butterflies, a bee, a stonefly, and dioecious plants" [1]. Butterfly species include *Brassolis sophorae* [2], *Polyommatus icarus* [3], and *Leptidea sinapis* [4].

Reproductive asynchrony can be a bet-hedging strategy against environmental stochasticity [5]. It has been shown that distribution of mating opportunities through time can avoid short-duration catastrophes and improve an individual's overall fitness. The magnitude of asynchrony is proportional to the variation typically realized in key environmental parameters like date-of-last-frost or timing of summer rainfall [6].

A previously beneficial life-history strategy can become a liability to a species under the wrong conditions, especially as anthropogenic forces generate ecosystem changes such as habitat fragmentation that can reduce the size of wild populations. Reproductive asynchrony can have a negative effect on the growth rate of small populations as individuals become isolated in time [7].

When a population's growth rate is reduced as population size decreases, an Allee effect can cause extirpation [8]. Loss of an entire population can occur due to the dynamic of positive feedback as population shrinkage and reduction in

reproduction reinforce each other. Knowledge of the relationship between population size and reproduction can be critical to conservation management.

Previous investigations of reproductive asynchrony have assumed that populations are well mixed spatially. Because real populations are often subdivided spatially and because individuals routinely disperse within their habitats, it is important to examine the consequences of this assumption of spatial homogeneity. Factors such as the spatial distribution of resources and behavioral details associated with mating are important biological complexities that can be considered in spatial models. We use computer simulations to investigate the quantitative relationship between population size and the loss of reproductive potential from asynchrony due to isolation in both time and space. The simulation is a spatially explicit, agent-based model.

1.2 The Allee Effect

As populations grow, their size approaches the 'carrying capacity' limit: the maximum population density that space and resources can support. Populations nearing their carrying capacity have a reduced per capita growth rate; this is called density-dependent growth. Inverse density-dependent growth occurs at the other end of the density scale. The decreased population growth that may occur in small populations is known as the Allee effect. The importance of Allee effects to behavioral, ecological, and conservation biology have only been recognized recently [9].

The Allee effect has been described for most major animal taxa [10]. Growth rates can suffer in small populations when individuals have a reduced fitness due to

2

the lack of conspecific support. Three major categories of contributing factors are: genetic inbreeding and the loss of heterozygosity, demographic stochasticity, and the loss of cooperative interactions [10]. Several specific examples from [11] follow. The workload per individual can drop in large populations. For instance, colonial male bluegill sunfish spend less time pursuing predators than solitary sunfish. Males with extra time will aerate their nest; this behavior reduces the incidence of fungal disease in their offspring. Another example is the case of plants that seed synchronously to satiate seed predators. This is a community behavior that increases each individual's fitness. Finally, at high densities, hemlocks can sequester water in the upper level of the soil and increase production [11].

The Allee effect can have important ramifications on conservation planning. The per capita growth rate of a species may be less than 1 below a specific density threshold (Fig. 1). A population reduced in size to near this threshold, but above it, may be able to recover naturally given time. A population that falls below the negative growth threshold will deterministically spiral to extirpation unless there is outside intervention. In a case like this, human efforts may be the only recourse for a dwindling species.
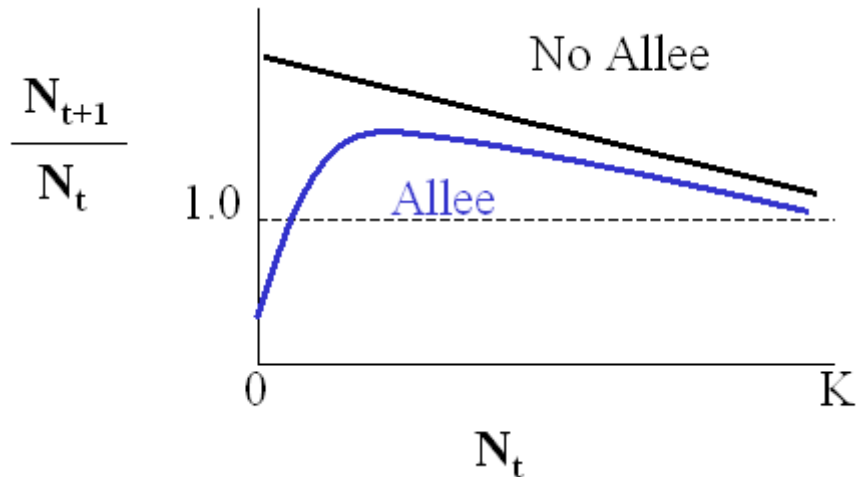
Figure 1: Allee Effect

1.3 Agent-Based Models

Agent-Based Models (ABMs) have been utilized in ecology since the late 1980s. In contrast to population-based models, which use averaged descriptors to summarize homogenous populations, ABMs expand the detail of modeling down to the individual. Increased specificity gives an ABM power and flexibility [12]. By simulating individuals, it is possible to assign them particular behavior patterns (e.g., movement rules) and distinct traits (e.g., some aspect of "quality"). Models of this type have demonstrated faithful recreation of many relationships in biology and population dynamics. Examples include: population growth, predator-prey interaction, and the effects of keystone predators [13].

Chapter 2: Simulation

We model mating interaction on a defined landscape. The scope of the model is a square grid 1000 units on a side. Specific units are not assigned to the simulation area. The important parameters affecting model results are the ratio of movement and detection lengths to the breadth of the population range; this is a dimensionless quantity.

Within the description of the details of the simulation that follow, the passage of time is described in time 'steps' or 'iterations'. General terms were chosen, because the simulation may be used to model any units of time. The results section will refer to 'days', because all simulation runs treated here use one day as the time step.

Individuals may represent any mobile species that exhibits reproductive asynchrony. Many of the behaviors that are explored in simulation runs are displayed by butterfly species.

The population is assigned a temporal window within which the aggregate of all members are reproductively active; each individual is assigned a sex (male or female) and a specific emergence time (i.e., time corresponding to the onset of reproductive activity) within the population-level mating temporal window. Each time step, individuals that are beginning their active period emerge in the simulation area. Reproductive potential is measured in all male-female pairs based on a proximity threshold. This pairwise overlap is calculated based on two metrics (see below). After the overlap measurement phase, movement is calculated for each individual.

For every permutation of parameters run, 500 replicate simulations were completed, with statistics calculated across replicates.

2.1 Behaviors

2.1.1 Hilltopping

Individuals of many species of butterflies and other insects have been known to aggregate at the tops of hills or at the location of other recognizable features of the landscape [14]; for example, *Papilio zelicaon* will seek high points [18]. Congregation in space such as this 'hilltopping' is modeled here to investigate the effect of non-random movement on the reproductive potential of the simulated population. Results from hilltopping runs of the simulation apply to other forms of aggregation. For example butterflies may also collect around host plants [15].

2.1.2 Host Plants and Clustered Emergence

Individuals may also be spatially distributed in a nonrandom manner due to their lifecycle and their interaction with the landscape. Incorporation of patchiness has become an important component in ecological modeling [16], because flora and fauna are rarely spread in a uniform pattern. Butterflies have a close relationship with their host plants [17]. Oviposition and adult-butterfly emergence may be spatially clustered because the host plants for the butterflies are themselves spatially clustered. In these modeling efforts, clustered emergence allows individuals to begin their active time period at one of a variable number of common locations in a heterogeneous landscape.

2.1.3 Female Mate Selectivity

In broad terms, male insects generally try to mate as often as possible, and females exercise discretion in selecting their mates. Females of the species *Callophrys xami*, for example, may continue their choice of mate even during mating activity [19]. This 'copulatory courtship' can result in the rejection of the male.

In these modeling efforts, this behavior is explored by assigning an attractiveness rank to each male that orders them from most to least attractive. One global parameter defines the percentage of the male population to which females will be receptive while they are selective. A second global parameter governs the fraction of the reproductively active time window during which all females are selective.

2.2 Emergence Location and Clustered Emergence

At the beginning of a simulation, each individual is assigned starting coordinates where they will emerge during the first time interval of their active period. For simulation runs with unclustered emergence locations, each individual is assigned a two-dimensional location, (x,y), where both coordinates are chosen from a uniform distribution with boundaries equal to the size limits of the simulated area. Thus, each individual is equally likely to emerge at every possible location.

Clustered emergence for simulations involving host-plants is determined by a parameter that defines how many emergence clusters are located in space. Each cluster is assigned a two-dimensional location, (x,y), where both coordinates are chosen from a uniform distribution with boundaries equal to the size limits of the simulated area.. Each individual is then assigned to a cluster location randomly with equal probability given to every cluster. Thus, during a simulation using a clustered

emergence parameter of 10, all individuals will emerge at one of 10 randomly

distributed points with an equal chance of each.

2.3 Emergence Time

The length of the time window in which individuals can become active is

defined as the total length of time in which individuals from the entire population

may be active during the simulation minus the length of the time period any

individual is active plus 1. Thus, if the population activity window is t=1 to 50, and

each individual will be active for 5 time steps, then the range in which any individual

may emerge and first become active is t=1 to 46. Emergence times are chosen from

the population level emergence window using a Beta distribution that creates

grouping in the middle of the emergence window [1].

2.4 Time Iteration Actions

2.4.1 Overlap

During each time step there is a distinct phase for calculation of overlap

between individuals followed by a phase for movement. During the calculation of

overlap each active female is treated individually. Each active female is compared

pairwise against all active males. The two-dimensional Euclidean distance between

each pair is calculated and compared to the Minimum Interaction Distance (MID).

MID is a global parameter defined for each simulation run. When the members of a

male/female pair are detected to be within the MID, the temporal overlap is recorded

for the female in two units. When the time step of the simulation is 1 day, the two

units of overlap are: days (called "time overlap") (Fig. 2) and male days (called "mate

overlap") (Fig. 3). Specifically, for a day during which a female is within interaction distance of 2 males, the female's time overlap is incremented by 1, and the female's mate overlap is incremented by 2.

Time overlap ratio = 3/5
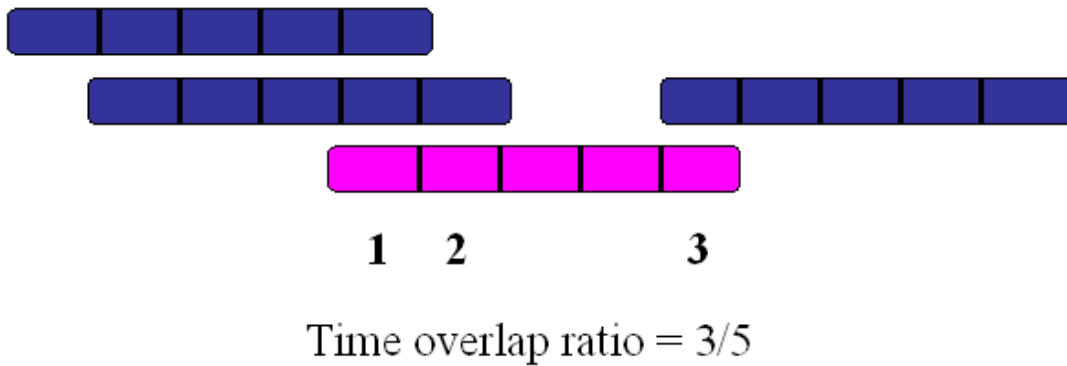
Figure 2: Time Overlap Metric

Mate overlap ratio = 4/5
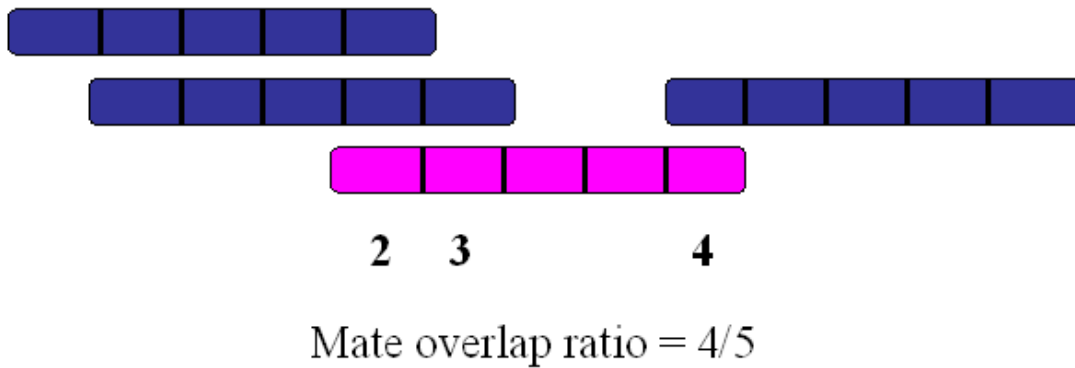
Figure 3: Mate Overlap Metric

2.4.2 Movement - Explicit versus Implicit

Movement is encoded into the simulation model in two ways. The general center of each individual's location changes each time step. This explicit linear

change in position on the landscape represents migration of the individual's 'home range' for the next time step (Fig. 4). At the end of each time iteration, an individual's location becomes the center of its home range for the next time step. Hereafter, explicit movement will just be called movement, and the center of 'home range' will be called location. A global parameter specifies the maximum linear distance individuals may move during one time step.

An implicit movement is represented as part of the MID. During the time step, individuals move between explicit locations, but not in a straight line. The random walk each individual takes may be much longer than their maximum movement distance parameter. MID accounts for the extra movement and allows individuals to encounter each other during the time step in a circular range around their location (Fig. 5).

Running the simulation with a large value for maximum movement and a small MID represents direct linear flight by individuals with little deviation. A large MID and a small value for maximum movement represents individuals that meander over a large proportion of the landscape during the time step and return close to their starting position by the end.
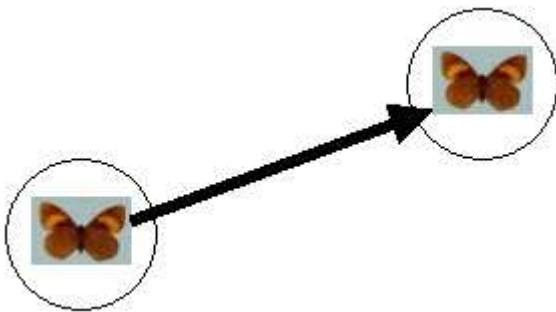
Figure 4: Explicit Movement
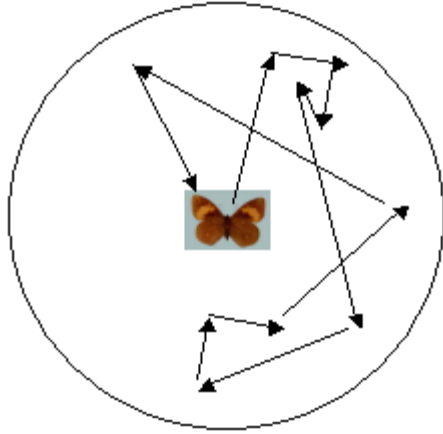
Figure 5: Implicit Movement

2.4.3 Movement - Algorithm

Random movement is executed by drawing horizontal and vertical distances from a uniform distribution. The distribution ranges from 0 to the maximum movement distance for the simulation. Horizontal movement is applied to the left or right with equal probability. The same is true for vertical movement. This results in a square of potential movement centered on the current location of the individual with sides twice the length of the maximum movement distance (Fig. 6). Every location within the square is equally likely to be the location the individual moves to during the time step.

During hilltopping scenarios, individuals will tend to aggregate near the center of the simulation space (Fig. 7). The hilltopping parameter defines how often movement during the time step is directly towards that goal. If the parameter is at 0.5, then there is a 50% chance each time step that the center of the individual's location will move diagonally toward the middle at the maximum movement distance. If this does not occur, the move will be random in both direction and distance as

described above. When an individual is closer to the center of the simulation space than its maximum movement distance, the location of that individual will be set to the center of the habitat.
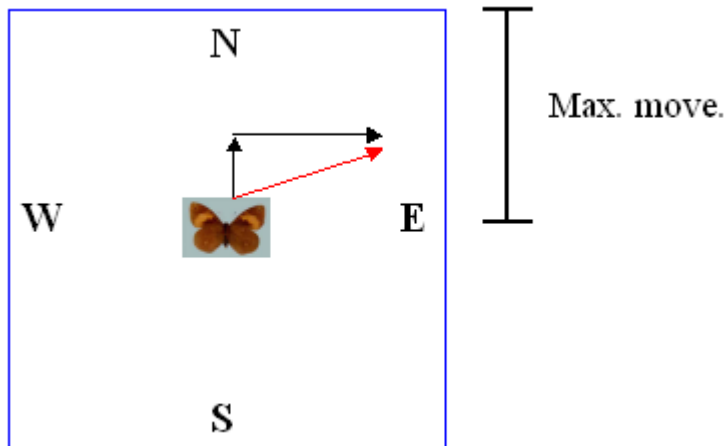
Figure 6: Random Movement
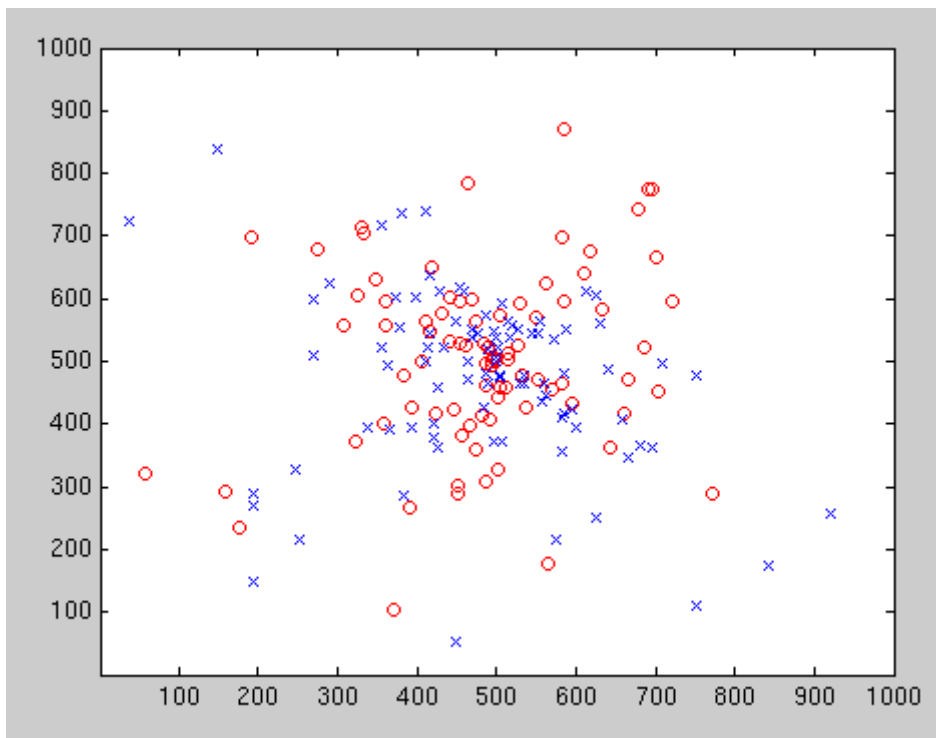
Figure 7: Distribution of Population During Hilltopping

2.5 Boundaries

For purposes of movement, wrap-around boundaries are used in this problem. Thus, individuals that move 10 units off the right edge will be placed 10 units to the right of the left edge and likewise for all other boundaries. Wrap-around boundaries prevent edge effects that might skew results by creating an unintentional build-up of individuals along the boundaries and increasing pairwise overlap. This scenario would occur, for instance, if individuals passing beyond the boundary were placed directly on the edge where they moved beyond it. Distribution of individuals would also be affected if movement was turned aside and continued along a boundary. The behavior of butterflies at habitat edges and the consequences of such behaviors on reproductive potential are of great interest to empiricists [20] and are worthy of future investigation by simulation.

2.6 Female Selectivity and Attractiveness Rank

Mate selectivity in this simulation is implemented to evaluate quantitatively the possible effects of female refusal on immediate reproductive potential. The treatment of the selective passage of genetic material and the resultant changes in fitness is outside of this scope. A possible model for female mate selectivity is a random percentage chance of acceptance on the occasion of each pair-wise overlap. This model has the drawback that refusal and acceptance are not based on any qualities of the male. The alternative that is implemented here instead is based on differential fitness between all males using an ordered hierarchy assigned to each male randomly. The fitness quality is not meant to correspond to any specific

morphological trait. Rather, it is a measure of how females respond to the particular

male during the courting process. We will call this value the attractiveness rank of

the male. Each male has a single attractiveness rank that is never altered during the

simulation. These are ordinal ranks ranging from 1 to the number of males.

During the overlap-calculation phase of the model, the female chooses to

accept or reject each male. Rejected males are ignored, and there is no increment to

either of the two measures of overlap; accepted males are counted normally.

Females may reject males during a beginning portion of their active window.

Two parameters define female selectivity as it is implemented in this simulation. The

selective period parameter defines the number of time steps at the beginning of the

active window during which all females exhibit selectivity. The acceptance ratio

defines the fraction of the male population that a female will accept during this time.

A typical usage of these parameters is acceptance ratio = 0.5, and selective period = 3

out of $w = 5$ time steps.

2.7 Statistics

Four statistics are calculated after each completed simulation. Average 'mate

overlap' is calculated as the number of male-time steps of overlap per each female

divided by the length of the active window averaged across all females. This number

can theoretically be as high as the number of males. Average 'time overlap' is the

number of time steps a female overlaps with at least one male divided by the length of

the active window averaged across all females. The maximum value of this metric,

which is the primary metric used for reporting reproductive potential, is one. The

'ratio unisolated' is calculated as the number of females with at least one time step of

time overlap during the entire simulation divided by the total number of females. The

'ratio mated' of females is statistical not deterministic. For each female, the time

overlap statistic is used to measure the cumulative exposure of a single female to a set

of males. The probability that the female is mated is its time overlap. Each female's

mating probability is compared against a random number drawn from a uniform

distribution from 0 to 1. The ratio mated of females is thus calculated as the number

of females mated divided by total females.

2.8 Implementation and Runtime

2.8.1 Pseudocode

Pseudocode for simulations is as follows.

Define:
Number of simulated values of parameter 1 = $\mathbf{p_1}$
Number of simulated values of parameter 2 = $\mathbf{p_2}$
Number of simulation trials = $\mathbf{m}$
Number of females = $\mathbf{N_f}$
Number of males = $\mathbf{N_m}$
Number of active females = $\mathbf{N_{fa}}$
Number of active males = $\mathbf{N_{ma}}$
Number of time iterations = $\mathbf{t}$

Loop through Parameter 1
    Loop through Parameter 2
        Loop through trials
            Set emergence location and time – $O(N_f+N_m)$
            Loop through time iterations

Loop through active females
Loop through active males
Measure pair-wise overlap – O(1)
Calculate Movement – $O(N_{fa}+N_{ma})$
Calculate statistics – $O(N_f)$
Average trials together – O(m)

The number of trials for each set of input parameters, m, is 500. Parameter 1 may have 10 or 20 values. Parameter 2 is generally the number of individuals, and it is frequently set to 10 different values. N_f and N_m range from 1 to 150 each, and they are set equal. Time iterations are generally 50 time steps representing days. The values of N_{fa} and N_{ma} are variable. They depend on the distribution from which the emergence times are drawn and on the ratio of the active window to the population level time window, t. Using 5 days active out of a total level of 50 for the population means N_{fa} is approximately equal to $0.1 * N_f$. While Big O Notation [21] for estimating the magnitude of runtime would generally disregard linear factors, the difference between N_f and N_{fa} is crucial in this simulation. The total runtime of the simulation varying 2 parameters is

$$O(p_1 * p_2 * m * t * N_{fa} * N_{ma})$$

Typical values of these numbers result in 10^8 trips through the center loop of the program. 'Touching' the records for all individuals during calculation of pairwise overlap will effectively change the runtime of the program to

$$O(p_1 * p_2 * m * t * N_f * N_m)$$

In this case, the size of each of the two innermost loops is on the order of N_f. Since $N_{fa} = 0.1 * N_f$, and the same is true for the males, this is approximately 100 times

greater in practice and increases the runtime of the program from hours to weeks.

Any method that needs to access each individual's record to determine if they are

active during the time step will render the simulation impractical to implement.

2.8.2 Sorting and Bookmarks

The algorithm must track the subset of individuals that are active and do it

without canvassing inactive individuals. A solution determined here involves

maintaining a separate list of males and females. Each list is populated with

individuals whose records are filled with emergence locations and times based on

chosen distributions as explained above. Each array is padded with an extra dummy

record that has an emergence time larger than any that will be used for real

individuals. Then, both arrays are sorted by their emergence time fields with the

extra record automatically sorted to the end. Preparing data structures with separate,

contiguous storage of all eventual male and female active subsets makes an efficient

heuristic possible. The male and female arrays are treated separately but in the same

manner.

Two bookmarks are placed on the array; they point to records based on their

index. Picturing the array and just the emergence time entries from left to right as in

Fig. 8, it can be seen that during any given time interval, the left bookmark points to

the leftmost of individuals who are still active according to the current time interval

and their own emergence time. The right bookmark points to the rightmost of the

individuals that have begun their active period the most recently.

The union of the record at the left bookmark, the record at the right bookmark,

and all records in-between constitutes the set of active members of the array. If both

bookmarks share the same record, the set of active individuals has just that one entry. If the left bookmark is to the right of the right bookmark, the set of active individuals is empty.

Pseudocode for moving the bookmarks:

array = array of emergence times of individuals

t=current time iteration

L=left bookmark index

R=right bookmark index

w=length of active window

As an example, if t=7, and w=5, then all individuals with emergence times from 3 to 7 inclusive will be active during time iteration 7 (Fig. 8).

The algorithm:

Initialize
  set L=1, R=0
For each time step from 1 to the maximum time step:
  while array(R+1) <= t
    R=R+1;
  end
  while array(L) < t-(w-1)
    L=L+1;
  end

      The left bookmark checks the emergence time of the record it points to, and it moves when that record is no longer active. The right bookmark checks one index to the right; it continues to move until the record to the right is not yet active. When a group of individuals share the same emergence time, the left bookmark will stop at

the leftmost, and the right bookmark will continue to the rightmost. Periods when there are no active individuals will automatically cross the bookmarks using this algorithm, and no access of records for checking pairwise overlap is needed.

It is important to note the default behavior of the 'for' loop which streamlines this approach. In the programming language used for this simulation, MATLAB, when a 'for' loop is called with a starting index higher than the finishing index and a negative step is not specified, the loop will abort without running any code within. Using this algorithm, the 'for' loops cycling through active males and then active females use the bookmark values directly with no bulletproofing or checks for special cases necessary.

The ordering and bookmarking algorithm slashes the runtime of the program by a factor of 100, which makes this simulation practical. The reduction in speed is due to three factors. Firstly, the heuristic rarely 'touches' array records for individuals that are not active. Active individuals are a small subset of all individuals, so this method greatly decreases the number of accesses to the array. Secondly, use of inactive records occurs at the beginning of each time step. These memory accesses occur several orders of magnitude less frequently than they would otherwise, because in this implementation they are called from outside of the centermost two loops of the algorithm. Finally, the array accesses are made to storage of sequential memory; this process is faster than access to data from disparate locations according to the 'principle of locality' [21].

19

2	2	3	5	6	6	8	9	9	1000

t=	2	2	3	5	6	6	8	9	9	1000
1	R	L								
2		L	R							
6		L				R				
7				L		R				
13								L	R	
14								R		L

Figure 8: Several Possible States of the Bookmarking Algorithm

Chapter 3: Results

3.1 Default Parameters

Unless defined to the contrary, the following parameter vales are used for simulations:

Spatial height = 1000
Spatial width = 1000
w/W = 5/50
Number of males = number of females
Temporal distribution = Beta
Emergence = unclustered
Movement = random
Female mate acceptance = 100%

Note: Error bars on all plots define a 95% confidence interval.

3.2 Isolating Temporal Effects

The simulation can be used to isolate the temporal effects of asynchrony on reproductive potential to provide a baseline null model against which the effects of the various spatial heterogeneities can be compared. The Minimum Interaction Distance (MID) quantifies the distance at which two individuals have the potential to meet and mate during a time step based on a combination of meandering during the time step and detecting each other. Setting the MID parameter to greater than s * sqrt(2), where s is the length of each of the sides of the square simulation area, ensures that two individuals can interact from any two locations within the simulation area. This setting for perfect mixing removes all spatial effects from the result.

Following a single curve in Fig. 9 through Fig. 12 shows the effects of asynchrony on different metrics of mating success under conditions of perfect mixing without spatial isolation.   As the population size increases, mate overlap grows linearly (Fig. 9). In contrast, time overlap (Fig. 10) and ratio mated (Fig.12), which is the probabilistic model, increase as a saturating curve. The ratio of unisolated females (Fig. 11) saturates much faster than does the time overlap statistic. The time overlap metric is the most direct measure of the amount of exposure each female has to potential mating; it will be used as the primary metric of reproductive potential in results that follow.

The "ratio active" is defined as w/W, which is the length of the active window for each individual divided by the duration of the total active period for the entire population. The graphs show the ratio active has a strong effect on time overlap.

Fig. 13 is a surface plot showing time overlap as a function of both population size and ratio active. The 'cliff' in the corner shows the compounding effect these two variables can have on reproductive potential.

Figure 9: Mate Overlap Ratio vs. Population Size for different values of w/W;
Movement = 500; MID = 1500

Figure 10: Time Overlap Ratio vs. Population Size for different values of w/W;
Movement = 500; MID = 1500

Figure 11: Ratio Unisolated vs. Population Size for different values of w/W; Movement = 500; MID = 1500

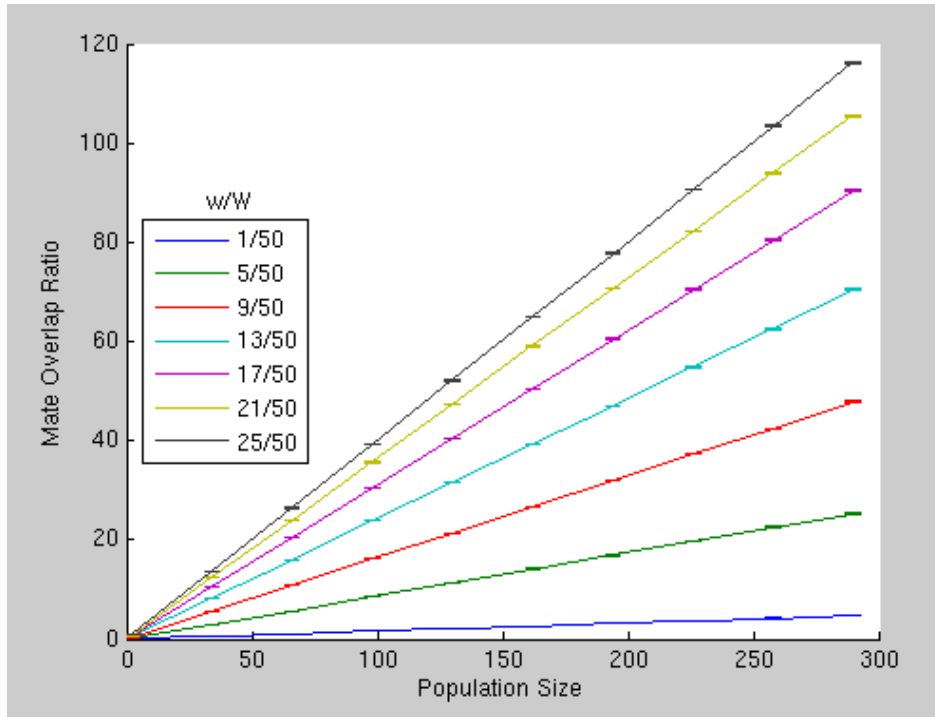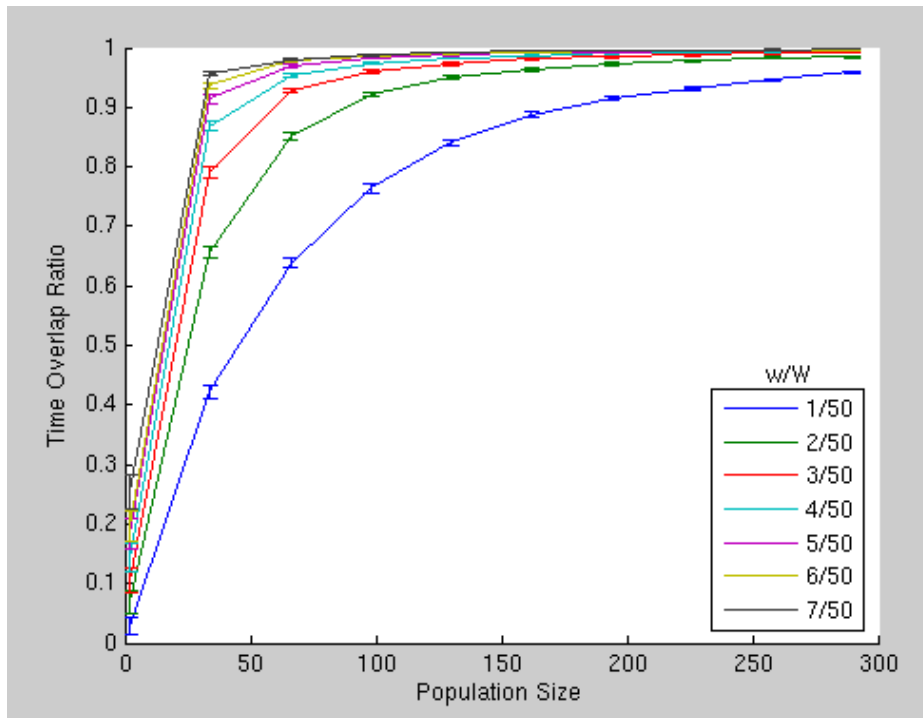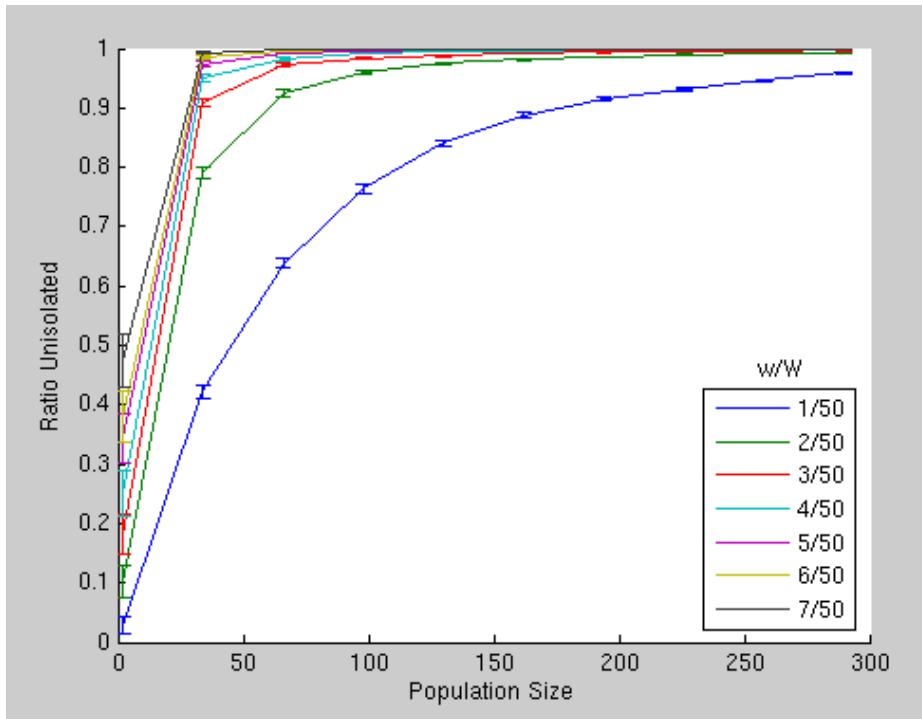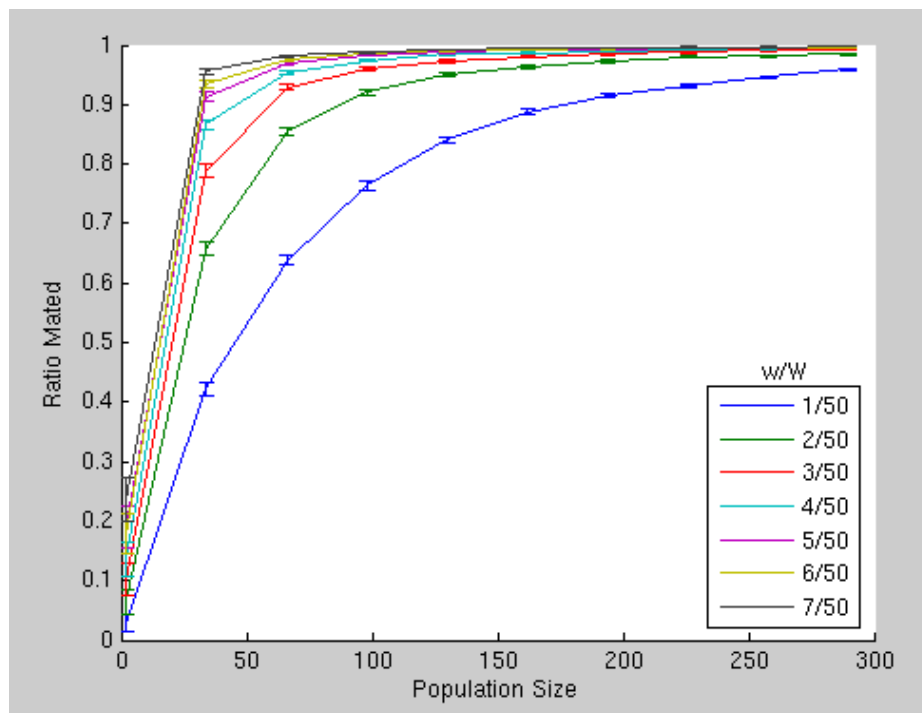Figure 12: Ratio Mated vs. Population Size for different values of w/W; Movement = 500; MID = 1500
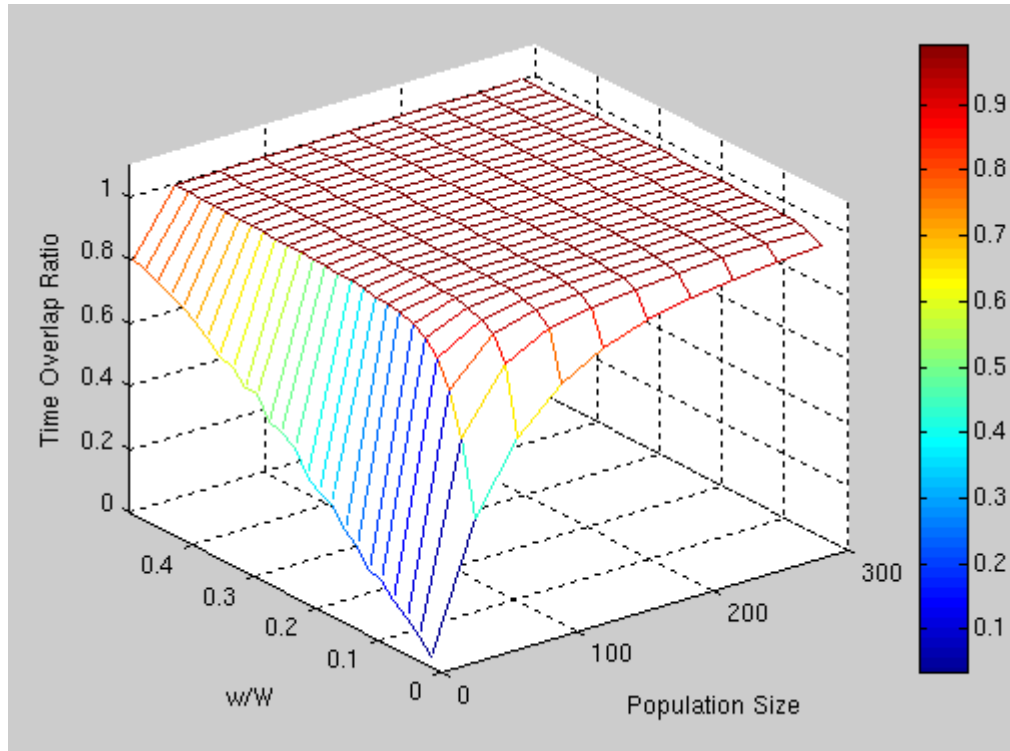
Figure 13: Time Overlap Ratio vs. w/W for different values of Population Size;
   Movement = 500; MID = 1500

3.3 Random Movement, Random Emergence

Including space in the modeling introduces two dynamic complications into

the model: movement and detection. To consider these complications, we examined

spatial effects on reproductive potential with and without temporal asynchrony. The

time overlap versus population size curve is compared for varying values of the

individuals' maximum movement distance and the MID.

3.3.1 Isolating Spatial Effects

Fig. 14 shows the time overlap for MID values varying from 100 to 500 in the

absence of any temporal asynchrony. The highest curve indicates that a MID value of

500 almost saturates the overlap statistic at 1.0. At this level, individuals in the exact

center of the simulation area will be able to interact and mate with individuals

everywhere in the landscape except the corners, whereas individuals not located

directly in the center will be isolated from at least a portion of the population (Fig.

15). That the time overlap saturates very quickly as a function of population size,

implies that effects from spatial isolation are not as strong as those from temporal

isolation.
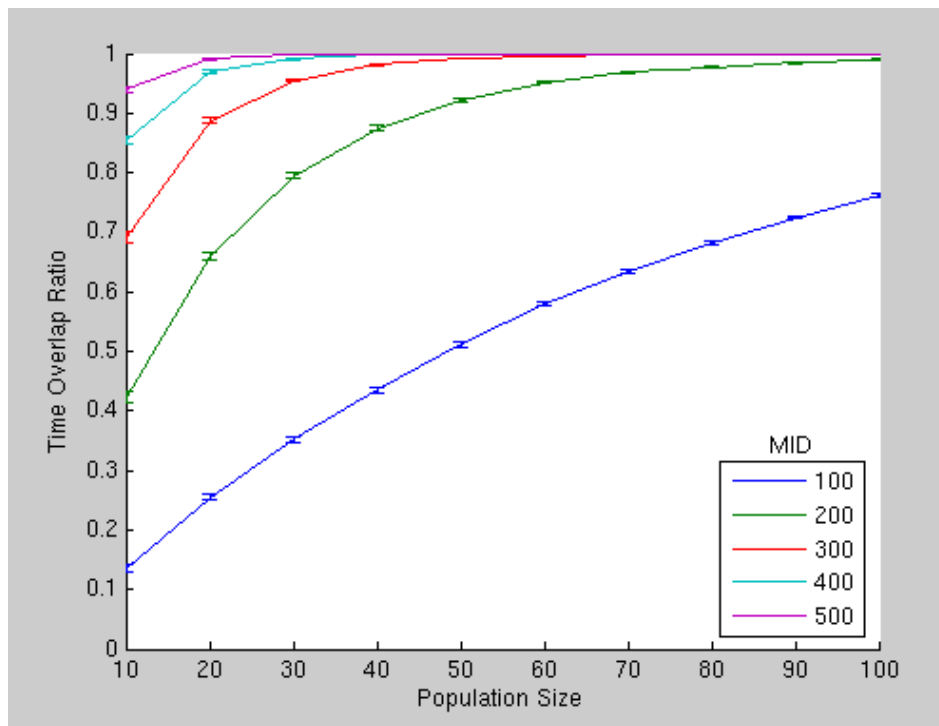
Figure 14: Time Overlap Ratio vs. Population Size for different values of MID;
    Movement = 500; w/W = 5/5 (No Asynchrony)
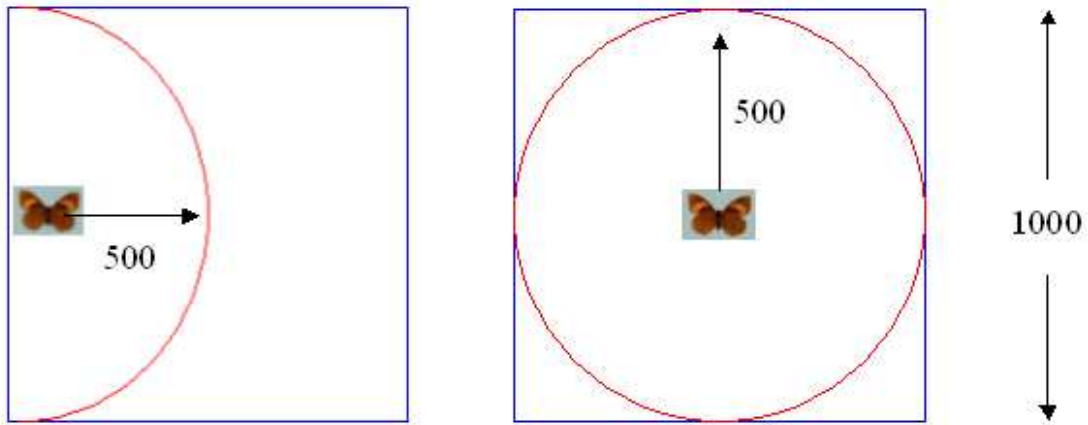
Figure 15: MID Parameter = 500

3.3.2 Temporal and Spatial Effects Combined

Fig. 16 shows the effects of the MID on the time overlap versus population size curve with reproductive asynchrony added. The top line represents the saturation curve for the temporal loss of reproductive potential (as judged by time overlap ratio) from a ratio active of 5/50; MID for this line is 1000. Curves below show the increasingly detrimental effect of reducing the MID. In simulations with curves with MID <= 500, individuals in the center of the simulation area cannot interact with individuals at the periphery. Fig. 17 shows a plateau; increasing MID beyond 800 has little effect.

We found that maximum movement distance had no effects on the dependence of time overlap on population size. Likewise, maximum movement distance had no effect on reproductive potential, which we found to depend only on population size and MID.

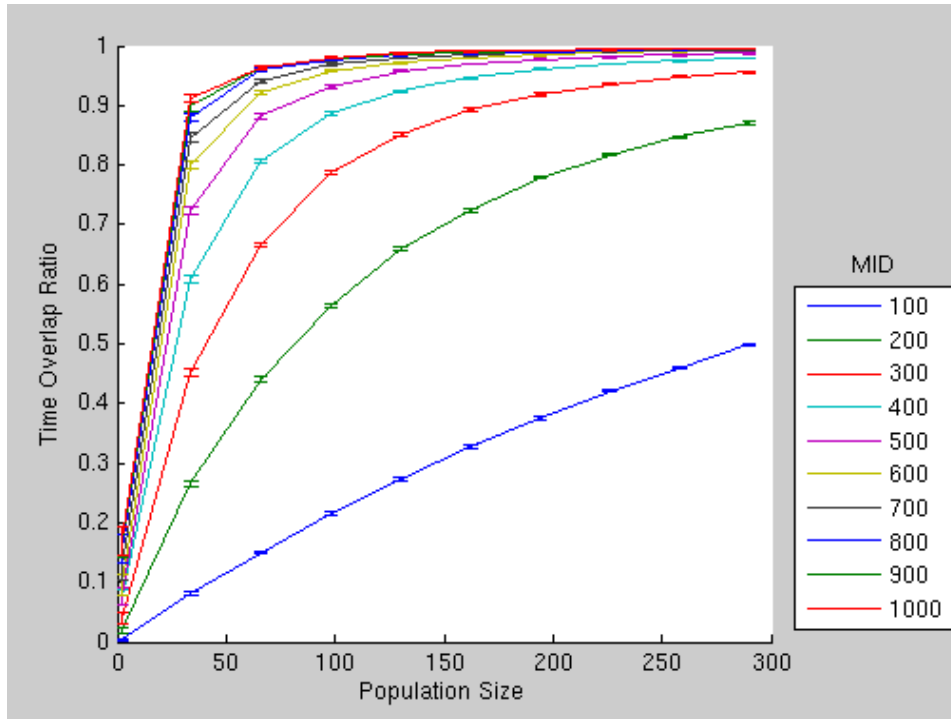Figure 16: Time Overlap Ratio vs. Population Size for different values of MID; Movement = 500
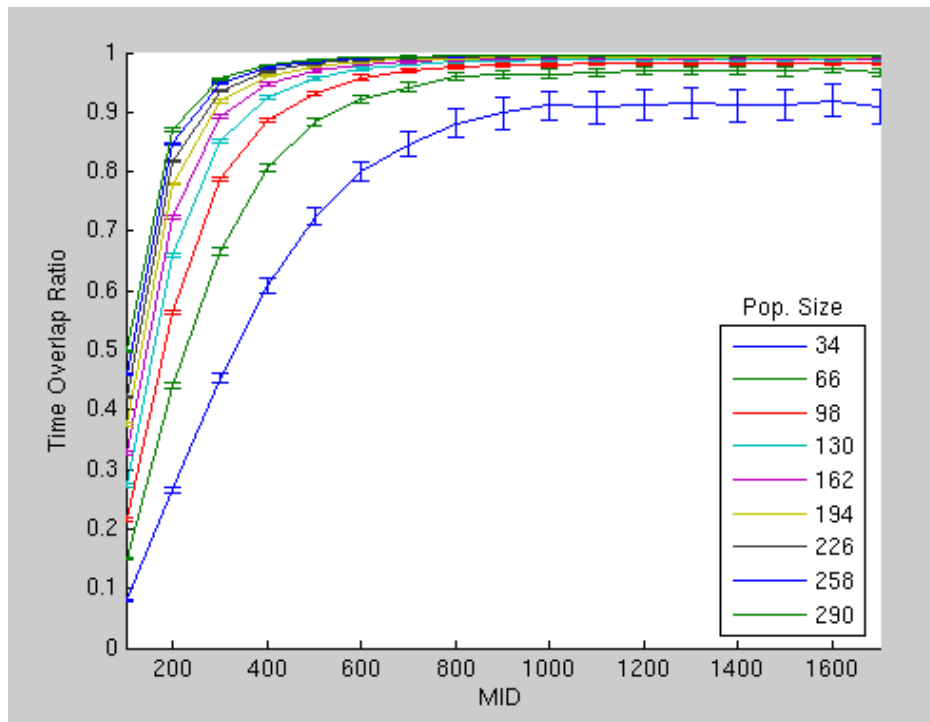

Figure 17: Time Overlap Ratio vs. MID for different values of Population Size; Movement = 500

3.4 Female Selectivity

Female choice in mating is an advantageous life history trait that may increase long-term fitness of offspring through selection of superior genetic material. This simulation measures the short-term loss in overlap potential resulting from female refusal of potential mates. Combinations of the following parameters are compared: the number of days that females show selectivity, the population size, and the ratio of males being accepted. Throughout these simulations, the movement distance parameter is set to 500.

3.4.1 Selective Days versus Population Size

The number of days that females were selective in mating was varied from 0 to 5 days out of 5 total active days. Each additional day added in which the female exercises discretion, the time overlap decreases by approximately the same amount (Fig. 18). The differential between the curves is larger in the center of the population size range, from about 40 to 140. Thus, female selectivity appears to have a smaller effect at extremes of population size.

Setting MID = 800 shows how selectivity can be detrimental to mating potential even when overall time overlap is very high (Fig. 19). Fig. 20 contains equivalency contours for the joint effects of population size and female selectivity. For example, a population of 110 individuals has the same reproductive overlap as one twice its size in which the females are selective.
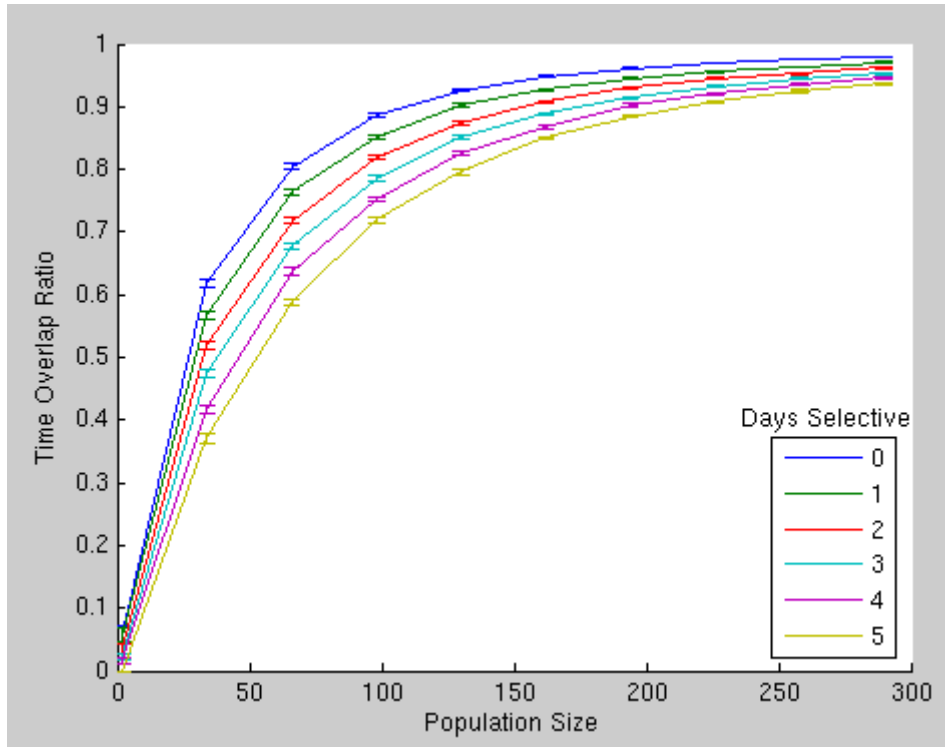
Figure 18: Time Overlap Ratio vs. Population Size for different values of Number of Days Selective; Movement = 500; MID = 400
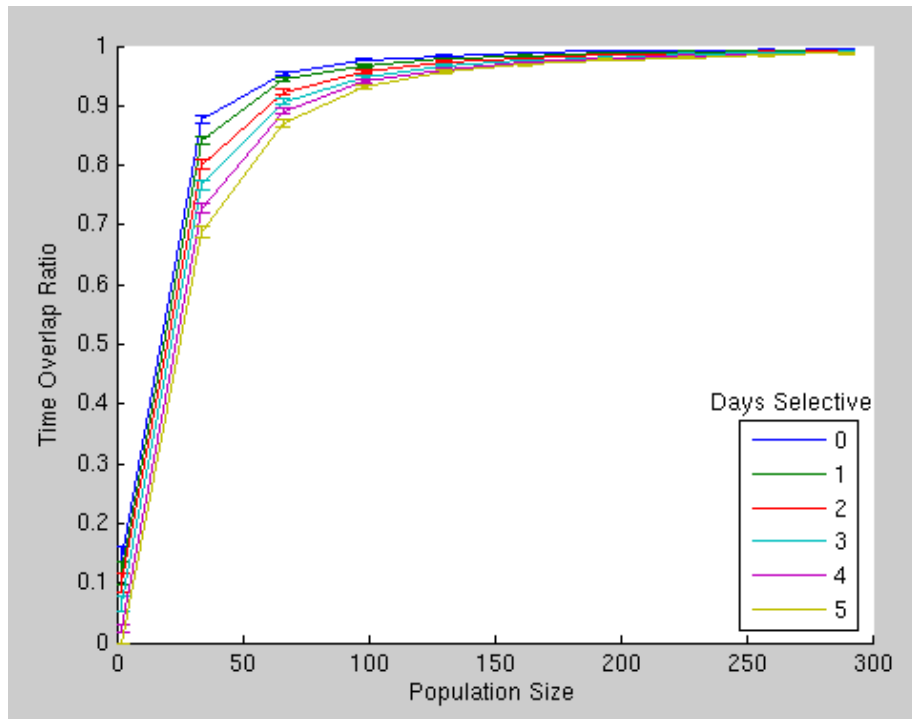
Figure 19: Time Overlap Ratio vs. Population Size for different values of Number of Days Selective; Movement = 500; MID = 800
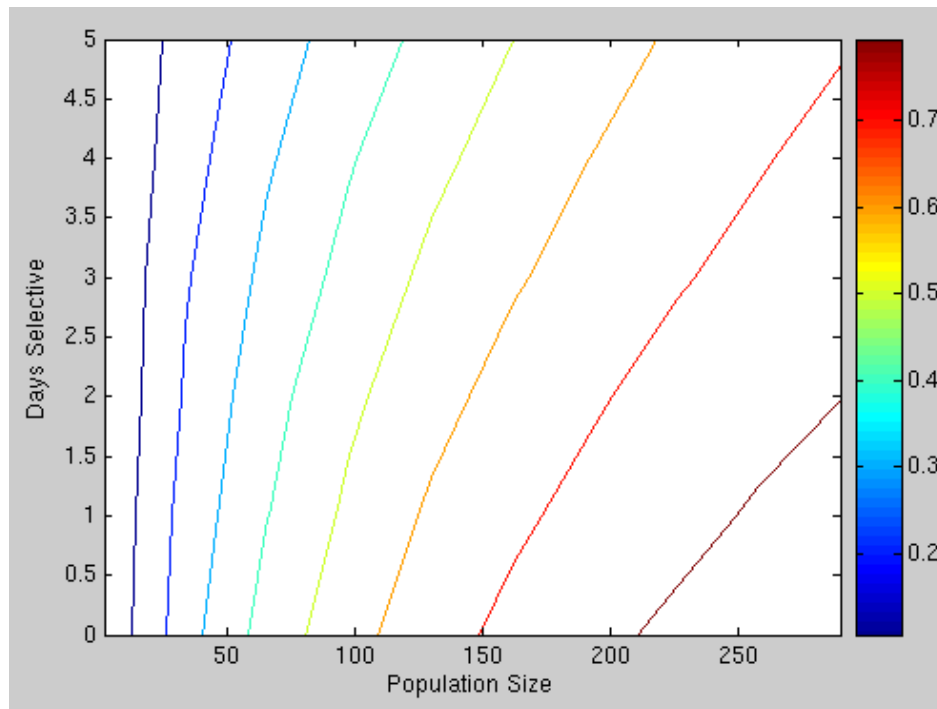
Figure 20: Contour plot for time overlap ratio as a function of Number of Days
Selective and Population Size; Movement = 500; MID = 200

3.4.2 Selective Days versus Ratio Accepted

Fig. 21 shows the relationship between ratio accepted and the number of days
the females are selective. Notice the distinct pattern: when the acceptance ratio is low
and females will mate with few partners, the number of days they display this
behavior has a large magnitude effect on time overlap. At high acceptance values, the
model shows that the number of days becomes unimportant.
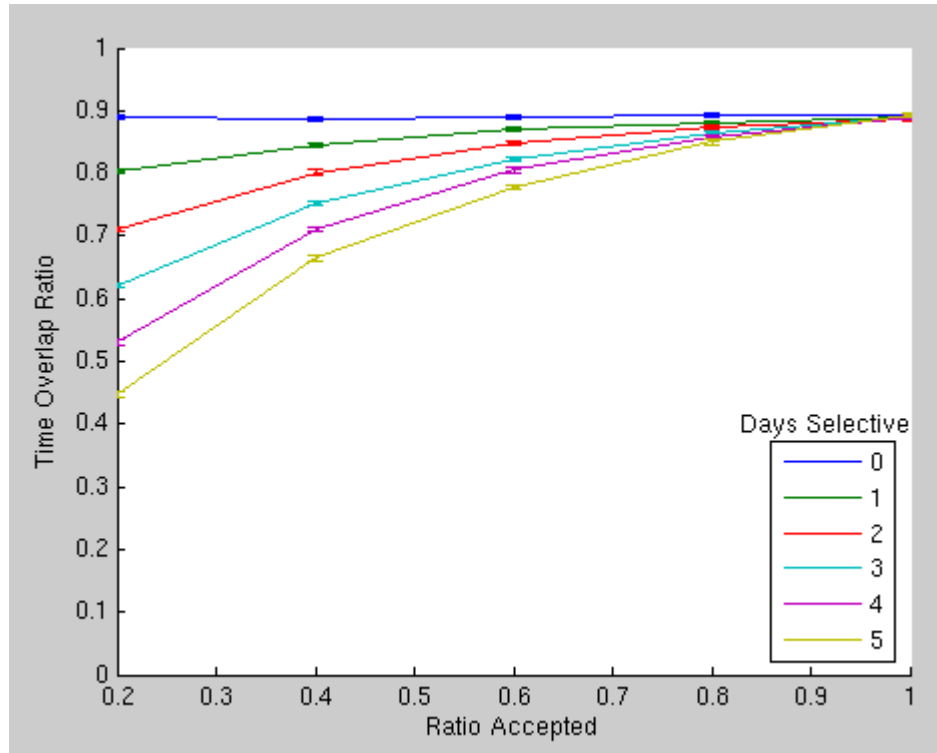
Figure 21: Time Overlap Ratio vs. Ratio Accepted for different values of Number of Days Selective; Movement = 500; MID = 400; Population Size = 100

3.5 Host Plant Emergence

Individuals emerging from common locations where host plants are located have a higher chance of sharing interaction space. Individuals emerging at the same host plant at the same time interval will always overlap for at least one time interval due to the order of operations within the algorithm. Overlap is calculated before the movement phase. The parameter of the clustered emergence algorithm is the number of clusters in the landscape.

3.5.1 Number of Clusters versus Population Size

Fig. 22 shows the time overlap versus population size curve for differing numbers of clusters. Simulations with 1-4 clusters show substantially increased time

overlap relative to the basic unclustered model (the equivalent of having each individual assigned to its own cluster). However, continued increases in the number of clusters yields diminishing returns in time overlap.

The simulation for Fig. 23 has MID set to 200. Overall, overlap is much lower due to the low interaction distance, but the benefit from clustered emergence has been magnified. At this lower MID value, numbers of clusters as high as 15 or 20 show an improvement over unclustered emergence. In Fig. 24, the maximum movement distance has been raised to 500; MID is still 200. Almost all benefit of spatially clustered emergences has disappeared. Effects from initial starting location have been swamped by dispersal because maximum movement distance is higher than the MID. Individuals that emerge from the same cluster a time step or two apart may no longer meet in the vicinity of their host plant.

Figure 22: Time Overlap Ratio vs. Population Size for different values of Number of
Clusters; Movement = 100; MID = 400

Figure 23: Time Overlap Ratio vs. Population Size for different values of Number of
Clusters; Movement = 100; MID = 200

Figure 24: Time Overlap Ratio vs. Population Size for different values of Number of Clusters; Movement = 500; MID = 200

3.5.2 Number of Clusters versus Maximum Movement Distance

Fig. 25 shows the relationship between the number of emergence clusters and the maximum movement distance compared to a base run that features no host plant clusters. This plot shows even more clearly the strong effect of movement on the benefits of clustering to the time overlap statistic. Small maximum movement distances mean individuals remain near their emergence location increasing local effective densities and facilitating mating success. As movement distances lengthen, individuals do not gain the benefit from clustered emergence. In the case of one

single cluster (green line), the positive change in overlap at movement=100 is 10

times greater than that of the benefit at movement=500.
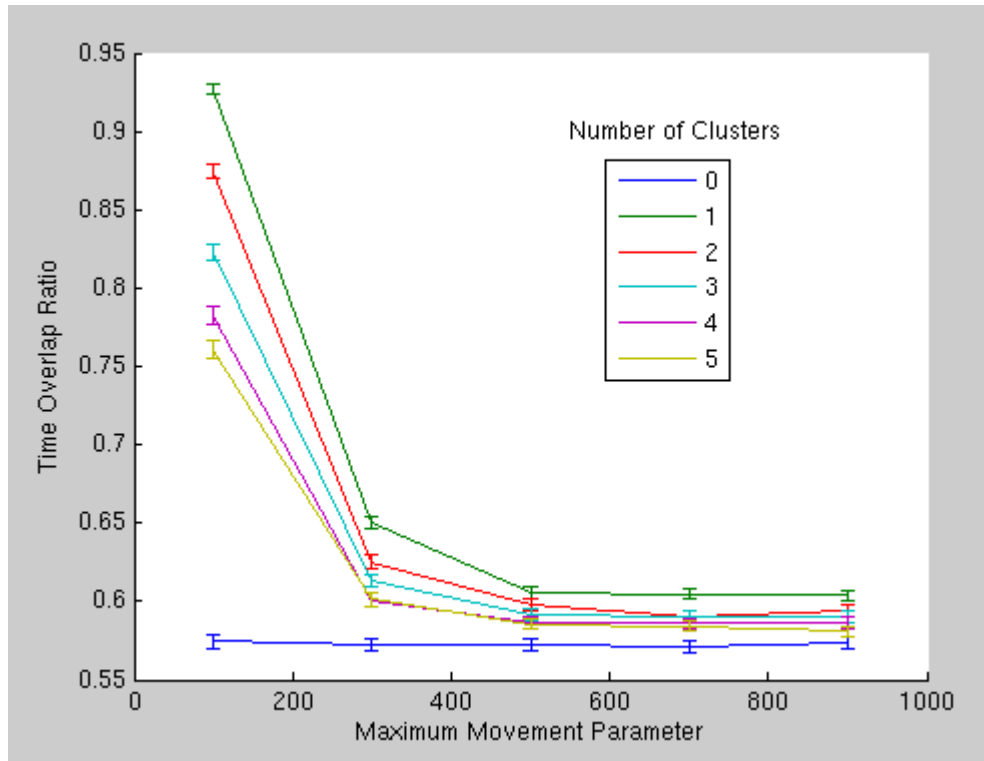
Figure 25: Time Overlap Ratio vs. Movement for different values of Number of
    Clusters; Population Size = 100; MID = 200

3.6 Hilltopping

The hilltopping algorithm is governed by movement bias, the parameter

controlling the fraction of individual movements that are directed toward the center of

the landscape.

3.6.1 Movement Bias versus Population Size

At high values of MID (Fig. 26), hilltopping shows a negligible increase in time overlap with increasing movement bias. In contrast, when MID is small (Fig. 27), hilltopping greatly increases the time overlap statistics, especially for small population sizes. Contour plotting shows the dramatic effect on average time overlap (Fig. 28). A population of 60 individuals with the maximum movement bias towards the center of the landscape has the same mating potential as a much larger population of 210 without hilltopping behavior.
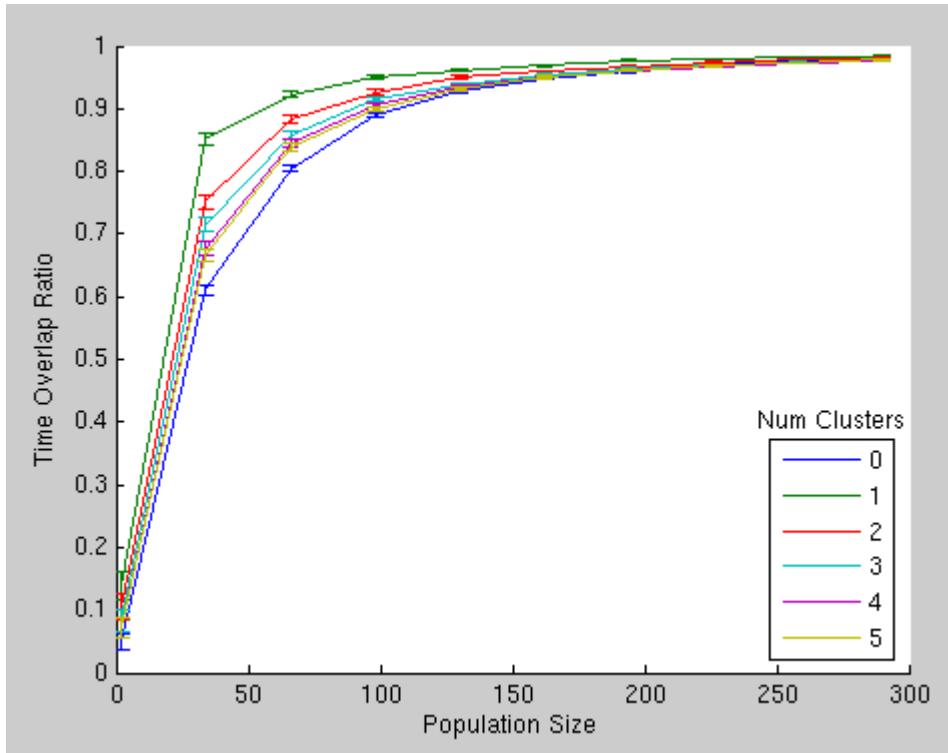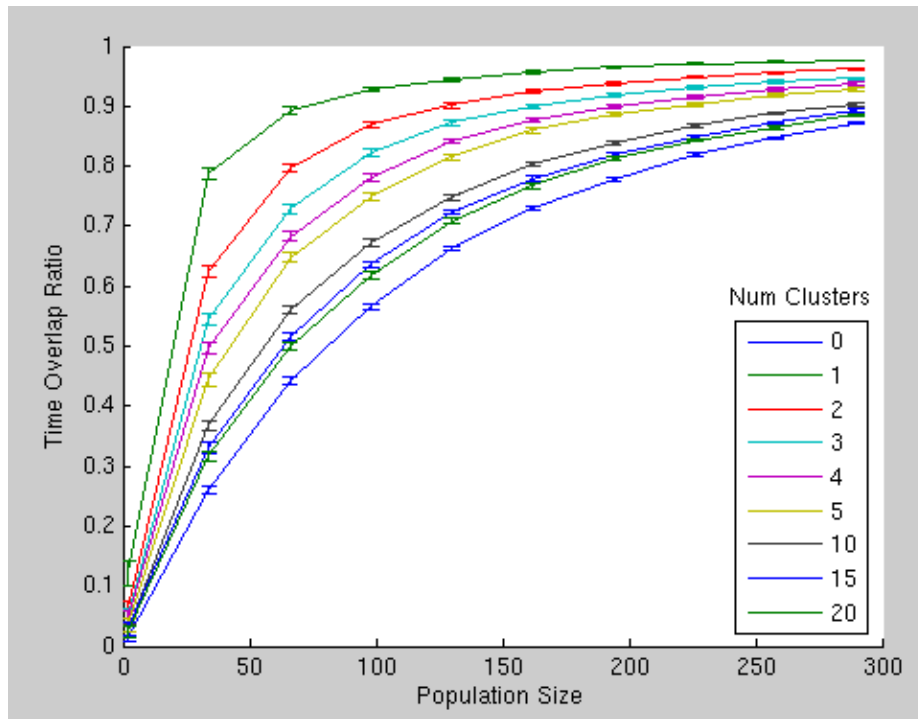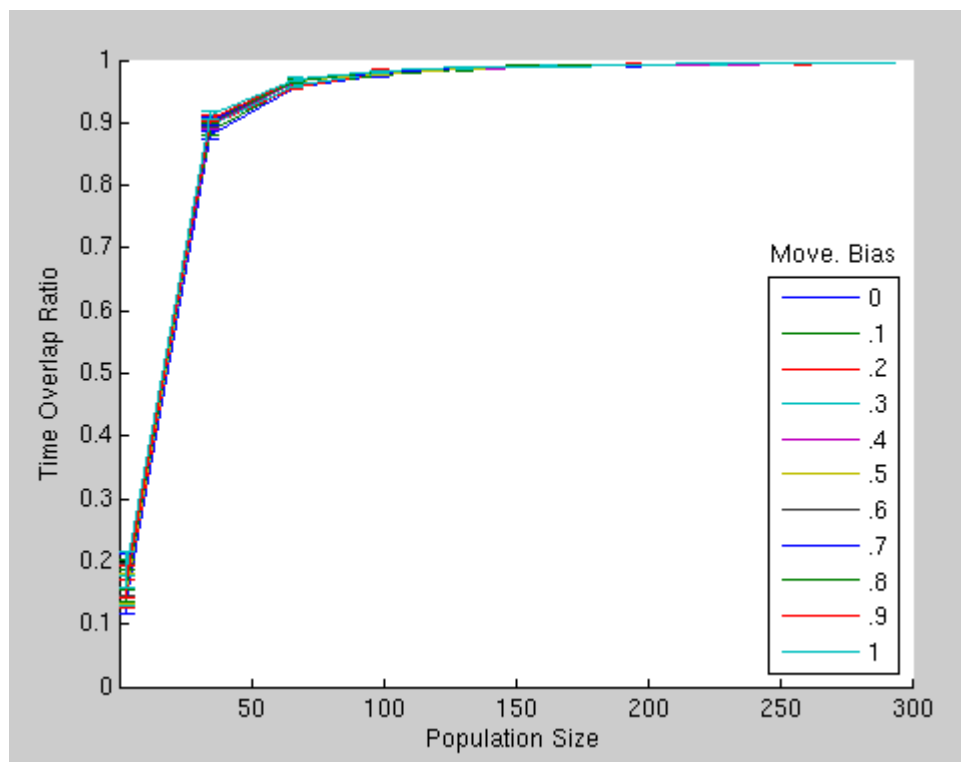

Figure 26: Time Overlap Ratio vs. Population Size for different values of Movement
    Bias; Movement = 500; MID = 800

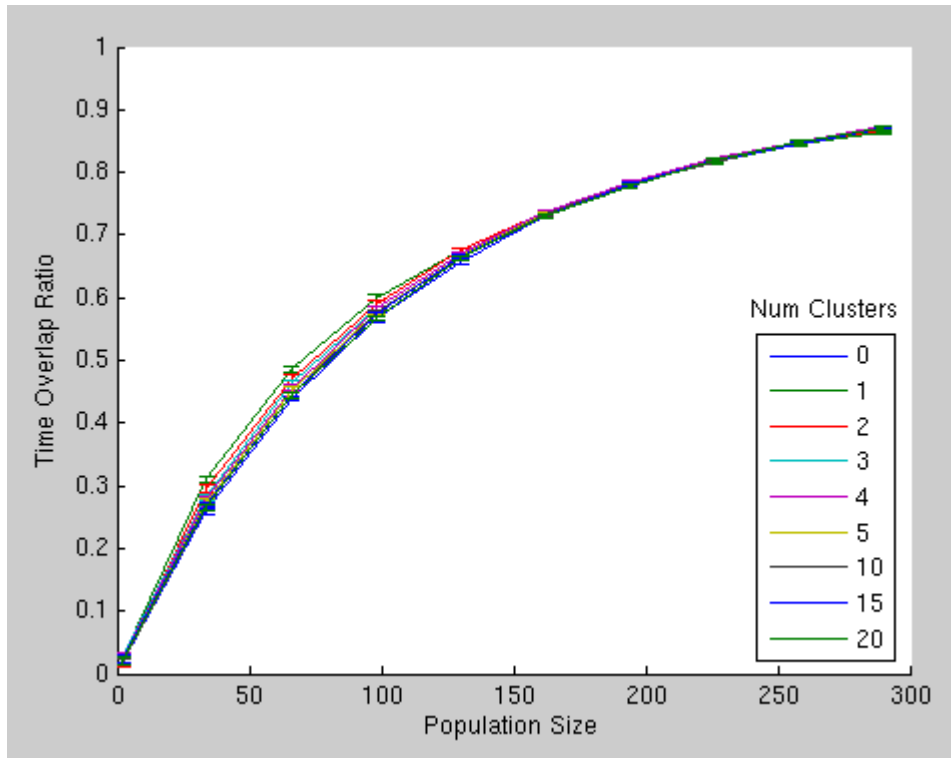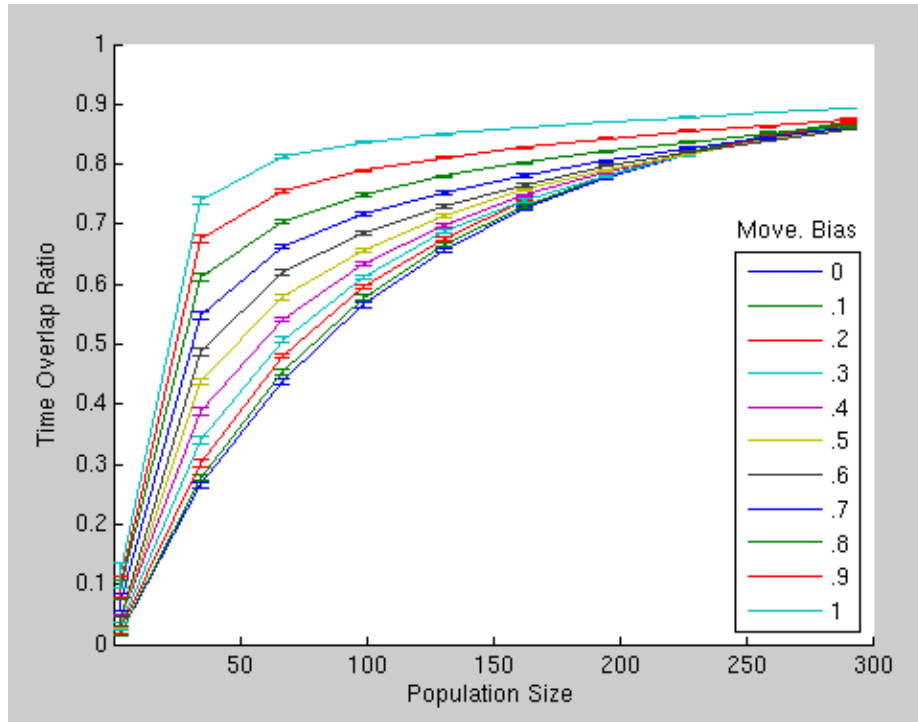Figure 27: Time Overlap Ratio vs. Population Size for different values of Movement Bias; Movement = 500; MID = 200
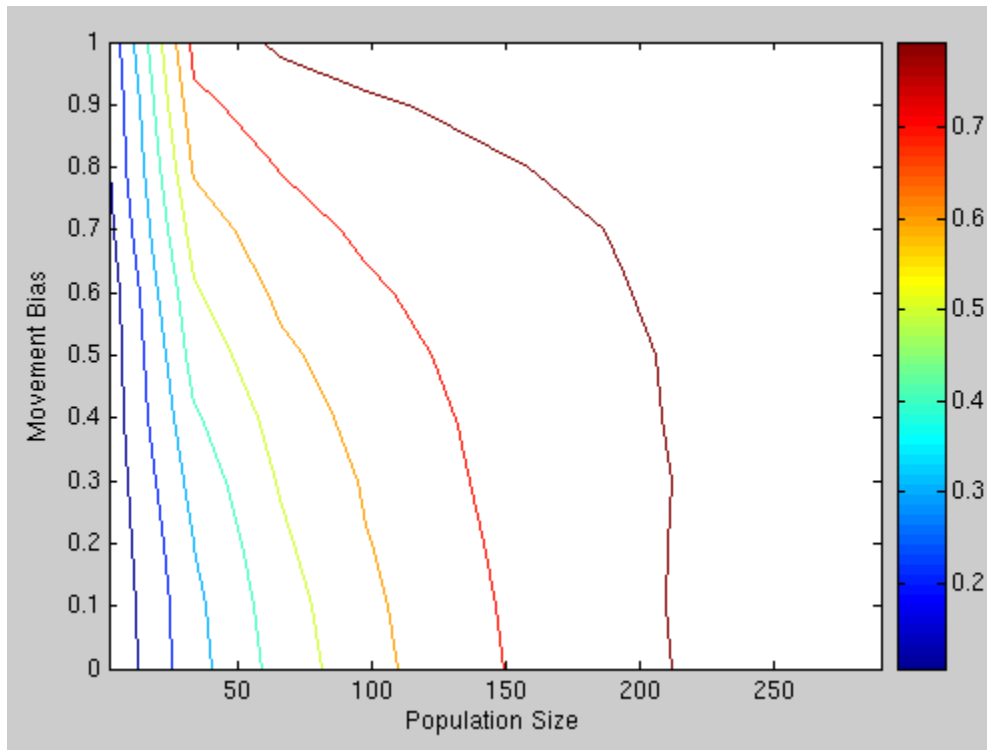
Figure 28: Movement Bias vs. Population Size for different values of Time Overlap Ratio; Movement = 500; MID = 200

3.6.2 Movement Bias versus Maximum Movement Distance

Above, movement distance changed the effects of life history strategies indirectly. Hilltopping is affected in a direct manner; the movement distance per time step governs how quickly individuals move toward their common goal in the landscape. Fig. 29 shows that the bias ratio is the most important factor in determining levels of overlap ratio, but movement distance can change the shape of the curve. There are two effects. At high levels of bias (lines near the top), a low movement distance will retard the benefits of the hilltopping behavior. The second effect occurs with low levels of bias. The overlap peaks at movement settings around 300, but then drops at high movement levels. The reason may be the inability of individuals to stay at the hilltop. There is a probability of $1 - b$ of random movement during each time step, where b is hilltopping movement bias. When the maximum movement distance is large, individuals moving randomly while they are on the hilltop will move farther away than the MID which for this run is set to 200. This simulation was run with populations of 100.
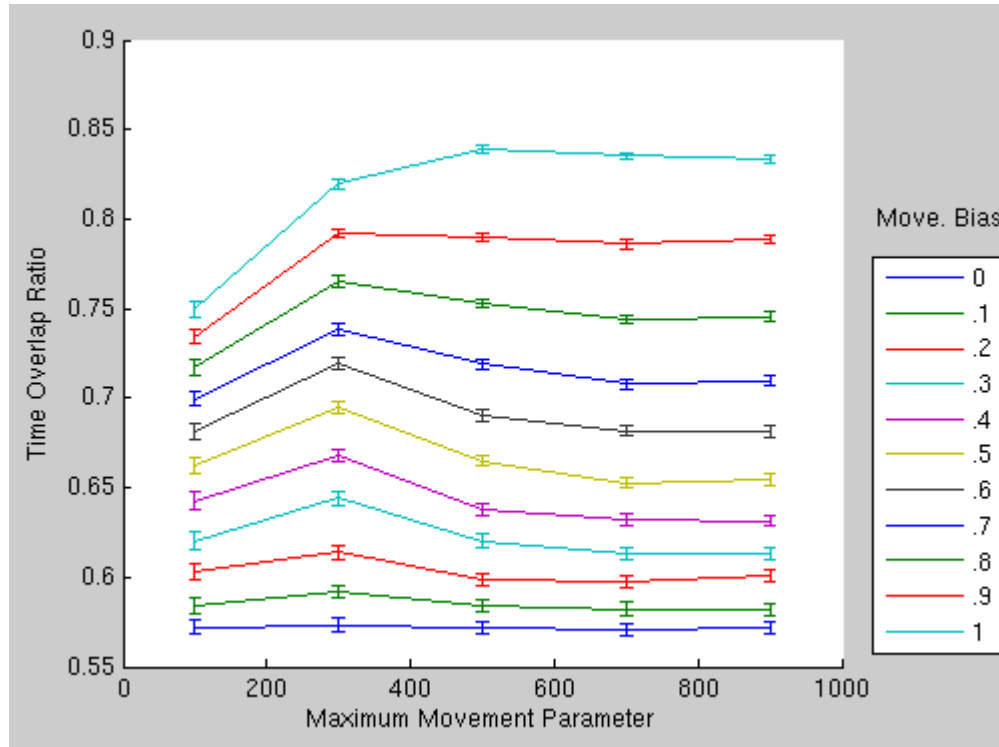
Figure 29: Time Overlap Ratio vs. Movement for different values of Movement Bias; Population Size = 100; MID = 200

3.7 Combinations of Life History Behaviors

Next, we examined the three spatial behaviors in pairwise combinations to access their relative effects on reproductive potential. For each simulation below, the results are based on populations of 100 individuals. The maximum movement distance is 500; the MID is 200.

3.7.1 Hilltopping versus Host Plant Emergence

As expected, high hilltopping bias and clustered emergence with smaller numbers of clusters are beneficial to the ratio of time overlap. As seen in Fig. 30, Hilltopping has more of an effect than the clustering does.
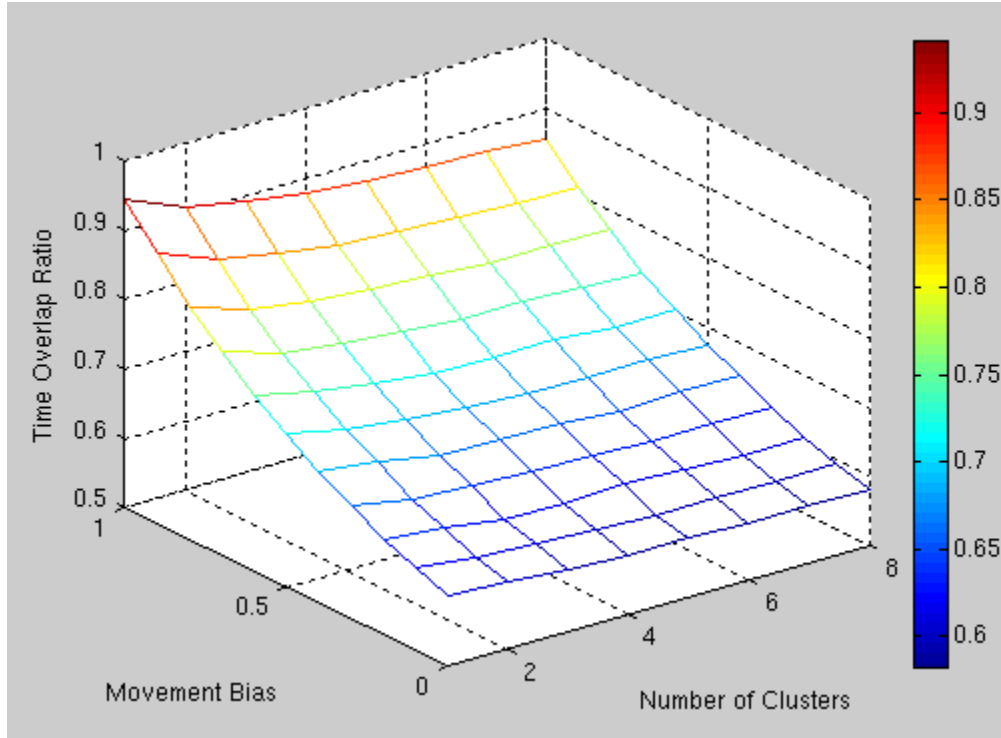
Figure 30: Time Overlap Ratio vs. Movement Bias vs. Number of Clusters; Population Size = 100; Movement = 500; MID = 200

3.7.2 Hilltopping versus Female Selectivity

Female selectivity in mating can counteract some of the benefit from hilltopping, but not all of it (Fig. 31). In addition, female selectivity has a more detrimental effect on mating success at small values of movement bias than at high movement biases. Isoclines in Fig. 31 show that when a female is selective in mating for all 5 days of her reproductive activity period but also has a movement bias of about 0.6, the positive and negative effects will cancel out. In this case the time overlap ratio is the same as if neither of these behaviors were present.

41
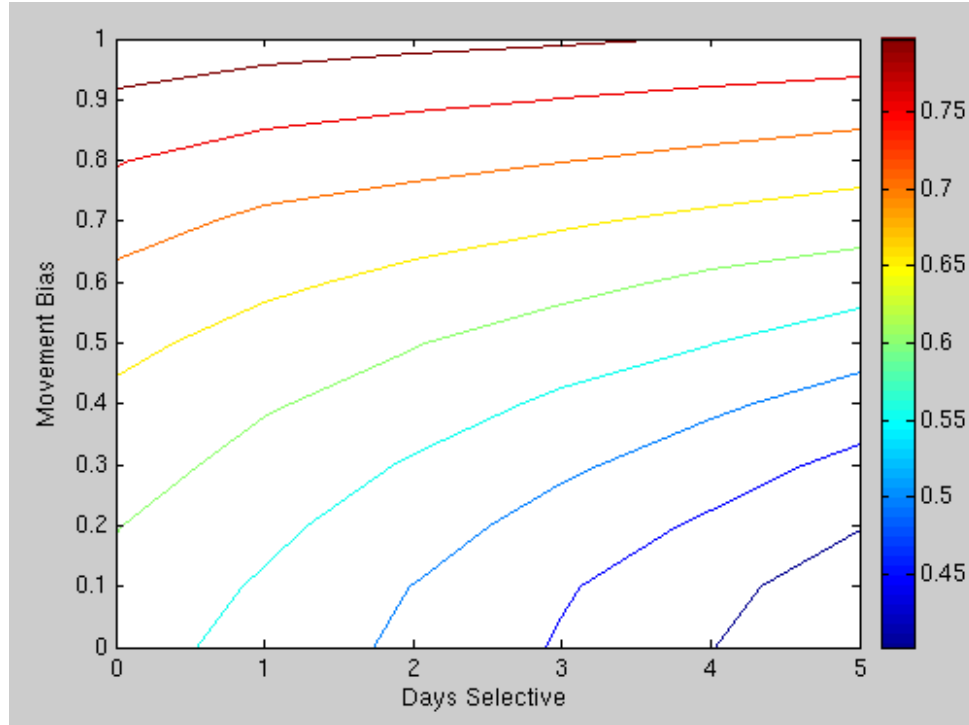
Figure 31: Movement Bias vs. Number of Days Selective for different values of Time
    Overlap Ratio; Population Size = 100; Movement = 500; MID = 200

3.7.3 Host Plant Emergence versus Female Selectivity

Clustering in emergence location does mitigate the negative effect of the

female selectivity, but only by small amounts (Fig. 32). The increase in time overlap

that results from clustering of emergence is slightly higher when females are selective

for a majority of their active days. Reducing the number of clusters from 8 down to 1

does not even improve time overlap enough to cover a single day of selectivity.
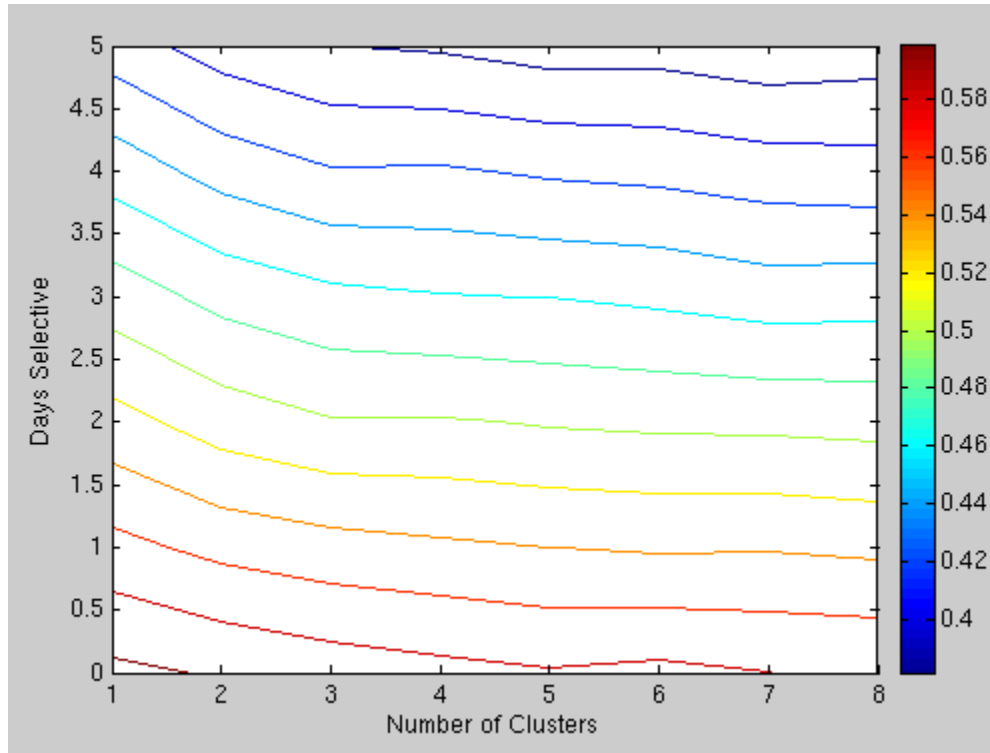
Figure 32: Number of Days Selective vs. Number of Clusters for different values of Time Overlap Ratio; Population Size = 100; Movement = 500; MID = 200

Chapter 4: Discussion

While reproductive asynchrony is a beneficial life history behavior in healthy populations, it can exacerbate declines in populations that are already struggling. Asynchrony has already been shown through computer modeling to have temporal effects on reproductive potential [1]. Our goal here was to quantify how much the addition of spatial isolation can worsen this loss of reproductive potential. We were particularly interested in using a spatially explicit model to explore the consequences of animal behaviors that might mitigate the effect of reproductive asynchrony. Relative to a spatially explicit model that lacked any behavioral detail, we found that two realistic behaviors (spatially clustered emergence and hilltopping) increased mating success under conditions of reproductive asynchrony but that female selectivity in mating decreased mating success.

4.1 Temporal Effects

Running the simulation with spatial effects removed demonstrated similar results to previous models that considered only the effects of temporal isolation [1]. Simulations with the MID set to a maximal value are equivalent to removing the spatial element from this model. In this case, asynchrony decreased reproductive overlap when overlap was measured both by the ratio of active days females spend with access to at lease one male (time overlap), and by the ratio of total male days to the number of days active (mate overlap). Asynchrony also affects the ratio of females that are completely isolated in time, and the number that are mated in a probabilistic model. The effects on reproductive potential are greatly changed by the

44

ratio w/W, which scales the length of the reproductively active window of an individual to the duration of the reproductive activity period for the population as a whole.

4.2 Intrinsically Spatial Effects

Introducing a spatial dimension to the model continues to degrade reproductive potential. Movement and interaction were quantified two ways. The first was overall linear movement of central location from one day to the next, which we called maximum movement distance. The second is the combination of multidirectional, noncumulative daily travel with detection called Minimum Interaction Distance. MID has a strong effect on reproductive potential. When it is small enough, individuals that are active during the same time may still not find each other and mate. As MID declines, time overlap declines quickly because the interaction area around each individual is dropping as the square of the MID. In contrast, the simulations demonstrated that daily movement had no effect on reproduction when movement was random. In cases where the population is spread uniformly throughout the landscape, there was no real advantage to moving farther every time step. Movement length had a strong effect when location or movement direction was not random.

4.3 Female Selectivity

In addition to separation in time and space, female choice can reduce reproductive overlap. Simulations have shown that this effect will be felt regardless of the current reproductive levels of a population. Both models with high MID and

high time overlap, and models with low values in those categories were affected. Female selectivity was not as strong as overall population size in determining overlap, but it made populations function as if they were smaller. The largest effects from this behavior occurred for populations of moderate sizes (40 to 140 individuals). The fraction of time that females were selective about mating was an important determinant of mating success only when females are receptive to fewer than half of the male population. As acceptance increased, the fraction of time that females were selective became unimportant.

4.4 Host Plant Emergence

As many studies have shown, patchiness and distribution of habitat is fundamental to population and community dynamics [16]. There is no reason to assume that emergence in this model should occur randomly. Host plants may tend to be clustered, and more than one individual will likely feed on and emerge from the same host plant. Clustering of individuals in this manner may alleviate some of the detriment of spatial separation.

Simulations demonstrated that spatial clustering could improve mate overlap, but only for limited cases. In active populations with a large MID, emergence must be concentrated to just a handful of host-plant clusters to have an effect on mating success. This constraint may be unlikely in populations with many members. Benefits from clustering emerged as the MID for populations went down. As daily, nonlinear travel decreased, the importance of starting location took precedence. In these simulations, individuals emerging from the same host plant shared a starting

location, but the host plants themselves were distributed randomly. Future models

that also cluster the clusters may show different behaviors.

Clustered emergence had the largest effect for mid-range population sizes (40-

140 individuals). This result may be due to the fact that populations that are very

large cannot improve by much, and those that are extremely small suffer from too

much temporal isolation to take advantage of spatial clustering. In contrast, the

benefits of host plant emergence were swamped by large movement values. In those

cases, individuals left their starting locations before others arrived. This may indicate

a biological benefit to maintaining some proximity to food plants.

4.5 Hilltopping

Butterflies in the wild tend to aggregate at distinguishable locations such as

hilltops [14]. This behavior can mitigate the potential for spatial isolation.

Hilltopping has proved to be the most influential of the behaviors examined here. It

affects small populations the most, implying that populations nearing extirpation may

increase their chance of survival with innate behaviors that bring individuals into

spatial proximity of one another.

In these simulations, hilltopping was helpful as long as the MID wasn't large

enough to provide temporal overlap without spatial aggregation, suggesting that

environment-cued movement may be more important in species that wander less.

Regarding maximum movement distance, simulation shows a bump in time

overlap values (see Fig. 29) when movement is large enough for individuals to travel

to a common destination but smaller than their interaction distance at the hilltop.

Clearly, a behavior strategy of aggregation in one place is ineffective if individuals

move away again instead of staying. Additional simulation might show whether this result is an artifact of the algorithm used.

4.6 Combination of Behaviors

The above behaviors have largely been studied separately from one another to ascertain their individual effects. However, some simulation runs combined these behaviors to see how they interacted. Clearly hilltopping and clustered emergence are beneficial while female mate selectivity is not in terms of the reproductive overlap metric. Hilltopping has the largest overall magnitude of change to overlap, followed by selectivity. Clustering has a lesser effect that occurs mostly when the number of clusters is very small.

The behaviors affect different-sized populations the most. Hilltopping provides the greatest benefit to small populations; the other two show the largest differential at mid-size populations of about 40 to 140 members.

4.7 Further Study

There are many options for continued study because of the flexibility of agent-based models. A few of these options follow.

Simulations can be continued for more than one generation. This approach would require modeling oviposition and host plant finding behaviors. There would be an opportunity to incorporate emergence clustering implicitly into these other submodels. The placement of groups of emergence clusters might show nonrandom relationships with each other much as patches of host plants are distributed in the

landscape. Modeling more than one consecutive generation would also allow metrics of extinction to be computed.

In the current model, within-day movement is assumed to be circular and evenly distributed. Smaller time steps make the runtime of the simulation prohibitively long. With the computers used, it is not likely that the size of the time step could be small enough to represent actual discovery and courtship behavior in a two-dimensional environment. As a substitute, it might be possible to measure the likelihood of any male-female pair encountering each other based on the beginning distance between them. The pairwise interaction could be segregated into a second submodel, which could be run over the gamut of possible beginning-of-encounter starting distances in advance. The results would be saved in a computer-accessible table and used in the main model. The difficulty to overcome is the method of selection of pairs in the main model. The submodel simulation of the interaction of all permutations of multiple males and multiple females from all possible starting distances is not feasible. The main model would need an algorithm to choose primary pairings, but hopefully without neglecting the lesser effects of other possible pairings on the overall outcome.

If the simulation were run using a smaller time step, it would be possible to use more definite movement algorithms. One example is a random walk with attraction between individuals that models an either-or behavior choice [22]. Individuals first check to see if they are in proximity to other individuals. When there is proximity, individuals aggregate. Otherwise, movement is random. Two other

interesting possibilities for movement types are the correlated random walk and the biased, correlated random walk [22].

More detailed depictions of the currently included behaviors might also be formulated. For instance, hilltopping might be a part-time behavior that individuals begin to favor if they remain mateless for some proportion of their reproductively-active window. Individuals might stray from the hilltop intentionally for a time and then return. Time steps smaller than a full day would make it possible for individuals to act differently in the morning and evening and to engage in perching and patrolling behaviors.

Adding detail and specificity to the simulation is an excellent way to focus its application, but one must also be aware of the loss of generality. A model of a specific species and ecosystem can provide focused findings for that region, but may lose applicability to other situations.

4.7.1 Real-World Data

Models are the most useful when they have a concrete basis in real-world data. A preferred relationship is a back-and-forth interaction in which field data informs the model, and the model makes predictions concerning testable results. This situation allows validation of the model, and in addition the model is more useful than one that is purely theoretical.

Temporal parameters governing this simulation were based on the literature review found in Calabrese and Fagan [1]. The w/W asynchrony ratio used here is a good representative value for observed behavior in many species.

Spatial values for this simulation need to be grounded in field data. The model was run with a wide spectrum of parameter values with the intention that all possible outcomes be examined. Further literature review may be able to narrow some of the parameter ranges or inform some of the behavioral dynamics. Specifically, a treatment of polyandry and fecundity in butterflies [23] will allow the incorporation of multiple matings into the model.

In addition, we believe that targeted field experiments may be able to ascertain values for the ratio of the radius of an individual's daily random movement to the extent of a population's range. In this case, the MID parameter in the model might be set to specific values; this would allow predictions of year-to-year population growth that might then be tested and used to validate the model. In the event the model proved accurate, it would then be used as the basis for a population viability analysis that would inform conservation management decisions.

4.8 Conclusion

Explicit spatial representation in a model of population dynamics shows that reproductive asynchrony can cause a loss of reproductive potential, and that the inclusion of two-dimensional space can exacerbate that loss. Temporal isolation in this model has more of an effect than spatial isolation, which may be due to the fact that individuals move and mix in space, but not in time. Aggregational behaviors have been shown to mitigate isolation in space.

The suite of simulations presented here represents a preliminary attempt to explore how temporal and spatial isolation interact to influence mating success. Opportunities exist for more extensive investigations of these questions using agent-

based modeling. As computers get faster, simulations can include all the iterations

wished for. The monte carlo style of these runs suits them perfectly to parallel

supercomputing.

Bibliography

[1]   Calabrese, J., and W. Fagan. 2004. Lost in Time, Lonely, and Single: Reproductive Asynchrony and the Allee Effect. The American Naturalist 164(1):25-37.

[2]   Carvalho, M. C., P. C. D. Queiroz, and A. Ruszczyk. 1998. Protandry and female size-fecundity variation in the tropical butterfly *Brassolis sophorae*. Oecologia 116:98-102.

[3]   Pollard, E., and T. J. Yates. 1993. Monitoring Butterflies for Ecology and Conservation: Conservation Biology Series. London, Chapman & Hall.

[4]   Warren, M. S., E. Pollard, and T. J. Bibby. 1986. Annual and Long-Term Changes in a Population of the Wood White Butterfly *Leptidea sinapis*. Journal of Animal Ecology 55:707-719.

[5]   Satake, A., A. Sasaki, Y. Iwasa. 2001. Variable Timing of Reproduction in Unpredictable Environments: Adaption of Flood Plain Plants. Theoretical Population Biology 60:1-15.

[6]   Post, E., S. A. Levin, Y. Iwasa, and N. C. Stenseth. 2001. Reproductive Asynchrony Increases With Environmental Disturbance. Evolution 55(4):830–834.

[7]   Augspurger, C. K. 1981. Reproductive Synchrony of a Tropical Shrub: Experimental Studies on Effects of Pollinators and Seed Predators in *Hybanthus Prunifolius* (Violaceae). Ecology 62(3):775-788.

[8]   Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders, Philadelphia, PA.

[9]   Hackney, E. E., J. B. McGraw. 2001. Experimental Demonstration of an Allee Effect in American Ginseng. Conservation Biology 15(1):129-136.

[10]   Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse Density Dependence and the Allee Effect. Trends in Ecology and Evolution 14:405-410.

[11]   Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee Effect for Behavior, Ecology, and Conservation. Trends in Ecology and Evolution 14:401-404.

[12]   Huston, M., D. DeAngelis, and W. Post. 1988. New Computer Models Unify Ecological Theory. Bioscience 38:682-691.

[13]   Simbiotic Software: Interactive Biology Simulations for Teaching and Research. http://www.ecobeaker.com.

[14]   Baughman, J., and D. Murphy. 1988. What Constitutes a Hill to a Hilltopping Butterfly? American Midland Naturalist 120(2):441-443.

[15]   Rutowski, R. 1991. The Evolution of Male Mate-Locating Behavior in Butterflies. The American Naturalist 138(5):1121-1139.

[16]   Fahrig, L., and J. Paloheimo. 1988. Effect of Spatial Arrangement of Habitat Patches on Local Population Size. Ecology 69(2):468-475.

[17]   Ehrlich, P., and P. Raven. 1964. Butterflies and Plants: A Study in Coevolution. Evolution 18(4):586-608.

[18]   Sims, S. 1979. Aspects of Mating Frequency and Reproductive Maturity in *Papilio zelicaon*. American Midland Naturalist 102(1):36-50.

[19]   Cordero, C. 1993. The Courtship Behavior of *Callophrys xami* (Lycaenidae). Journal of Research on the Lepidoptera 32:99-106.

[20]   Ries, L., R. Fletcher Jr., J. Battin, and T. Sisk. 2004. Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. Annual Review of Ecology, Evolution, and Systematics 35:491-522.

[21]   Bryant, R., and D. O'Hallaron. 2003. Computer Systems, A Programmer's Perspective. Pearson Education, Upper Saddle River, NJ.

[22]   Turchin, P. 1998. Quantitative Analysis of Movement. Sinauer Associates, Inc., Sunderland, MA.

[23]   Torres-Vial, L. M., M. C. Rodriguez-Molina, and M. D. Jennions. 2004. Polyandry and Fecundity in the Lepidoptera: Can Methodological and Conceptual Approaches Bias Outcomes? Behavioral Ecology and Sociobiology 55:315-324.