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MARK K. WOEHRER
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SEXUAL SELECTION, RESOURCE DISTRIBUTION, AND GENETIC DRIFT IN SIMULATED ECOLOGICAL SPECIATION

A DISSERTATION APPROVED FOR THE
SCHOOL OF COMPUTER SCIENCE

BY

Dr. Dean F. Hougen, Chair

Dr. John K. Antonio

Dr. Sridhar Radhakrishnan

Dr. Thomas S. Ray

Dr. Ingo Schlupp

To my father, Leon Woehrer.

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Abstract

True interdisciplinary research is difficult to classify as belonging to one field or another. Many of the interesting research areas lie on the boundaries of our current research communities. By working on common interests biological and computational scientists can synergistically develop new forms of computation and models of biological phenomena.

Speciation is one of the most fundamental processes in evolutionary biology. This concept is largely unexplored and has yet to reach its full potential in artificial life, evolutionary computation, and evolutionary robotics investigations. Traditionally, speciation was mainly viewed as allopatric speciation. More recently, another mechanism of speciation has been studied that does not require geographic isolation.

This raises a number of interesting questions, some of which we are addressing in our simulation study. The first question is whether or not the existence of differences in resources will lead to divergence and speciation. Second, what is the role of female preferences? Would they potentially strengthen or weaken divergence?

Four hypotheses were formed and evaluated using the same experimental conditions in a simulated environment inspired by life on the Galapagos islands. In particular, the wet and dry season dynamics were modeled to produce the intense selection pressure found on the islands. Both large and small populations of seeds and hence large and small populations of birds were considered in our experiments.

Our results provide direct evidence for the proposed hypotheses. The most interesting case is when assortative mating is combined with uniform random seeds in which we found pseudo-speciation. With larger population sizes we found similar results with a reduced genetic drift component for the uniform seeds and assortative mating case.

In this dissertation we have addressed interesting questions related to mate selection in

our ecological simulation and provided significant contributions with our work. By focusing on one phenotypic trait, we found that our simulated bird populations evolved specialized beaks for the food resources available and that sexual selection based on assortative mating was necessary for speciation. This research suggests to researchers in artificial life, evolutionary computation, and evolutionary robotics some of the mechanisms that may be utilized to foster artificial speciation.

CHAPTER 1

Introduction

1.1 Motivation

True interdisciplinary research is difficult to classify as belonging to one field or another. The primary goal of this dissertation was to find shared goals between biological and computational scientists and to use that synergy to develop models and hypotheses about speciation.

Recently, at a NSF-sponsored workshop, researchers from both biological and computational sciences discussed how shared principles could help foster a new era of cross-disciplinary research. In support of this workshop, the NSF posted a “Dear Colleague Letter” (Roskoski and Jahanian, 2011) reinforcing the importance of sustained, synergistic collaborations between the two fields.

Many of the interesting research areas lie at the intersection of our current research communities. By focusing on these common interests, biological and computational scientists can harmoniously work to generate new theories of computation and a better understanding biological phenomenon.

At the workshop, the biologists and computer scientists were asked to discuss how specific problems might benefit from collaboration related to shared principles. In the workshop report (Greenspan et al., 2010), a number of areas were identified including flexible pattern recognition and artificial neural networks.

The connection to this dissertation is clear. Flexible pattern recognition and advances in neural networks would benefit the recognition of possible mates, the identification of predators and food, and learning. In addition, we believe that speciation, a hallmark of biological system has been under-explored by computer scientists and in particular the artificial life community.

Although our goal is true interdisciplinary research, this dissertation is mainly concerned with speciation and its future application to artificial life, evolutionary computation, and evolutionary robotics.

Speciation is one of the most fundamental processes in evolutionary biology. It is the way biodiversity is created and a phenominon that has intrigued biologists since Charles Darwin's time.

Traditionally, speciation, the splitting of one species into two, was mainly viewed as allopatric speciation. Here, populations of a single species are geographically isolated and evolve independently in their disjunct habitats. Over time they become separate species that, even after secondary contact, and do not interbreed.

More recently, another mechanism of speciation has been studied that does not require geographic isolation and is based on differences in how individuals of an existing species use ecological niches. Under this mechanism, speciation occurs while the budding species live together in sympatry, gradually using different niches. The existence and possibility of such processes have long been unclear, but recent theoretical, observational and experimental studies have made it clear that this so-called sympatric or ecological speciation is more common than previously thought (Coyne and Orr, 2004; Seehausen and van Alphen, 1999).

This raises a number of interesting questions, some of which we are addressing in our simulation study. The first question is whether or not the existence of differences in resources will lead to divergence and speciation. If, for example, seeds of discrete different sizes are available for a population of birds, will the birds track the resources, evolve specialized beaks, and eventually diverge into separate species? Alternatively, what is the role of female preferences? Would they potentially strengthen or weaken divergence? The role of female mate preference has attracted recent attention and we use our model to explore some aspects of this.

1.2 Background

The model we selected was informed by studies on Galapagos finches by Peter and Rosemary Grant (Grant and Grant, 1987). The Grants are evolutionary biologists who studied the evolution of Darwin's finches in the Galapagos islands (Weiner, 1995), a group of volcanic islands near the equator. In their decades-long study on Daphne Major, an island just north of Santa Cruz, they carefully documented the process of evolution in populations of ground finches by taking measurements of beak size along with other physical attributes. The beak size is of great importance because it has the highest variability which is essential for evolution (Darwin, 1859).

The Grants were not the first visitors to the islands. A long line of explorers, naturalists, and researchers have visited the islands. Most researchers before the Grants visited the Galapagos islands during the wet season. During this interval, birds with with large beaks and small beaks typically eat the same seeds. This is curious because birds with larger/stronger beaks such as the Large Ground Finch *Geospiza magnirostris* are better adapted for larger, harder-to-open seeds.

1.3 Overview

In this simulation study, we investigate in situ speciation of artificial finches that feed on artificial seeds more or less effectively based on beak size. This experiment will be quickly recognized by biologists as reminiscent of "Darwin's finches" on the Galapagos Islands. Here, the evolutionary process consists of natural selection followed by sexual selection. Natural selection removes individuals from the population while sexual selection in combination with reproduction adds new offspring. Natural selection and sexual selection can work together to modify a population so that it becomes better adapted to its environment over time.

In this work various characteristics of the Galapagos islands and its famous birds are simulated. Daphne Major is modeled as a square region and contains two simulated objects, birds and seeds. Each individual has certain properties including age, beak size, energy level, and gender while each seed has a particular amount of energy, location, and size.

1.4 Hypotheses

For the speciation experiment we picked two sexual selection methods, assortative and random, and two environmental conditions, bimodal and uniform random seeds. Our first motivating question was whether or not the existence of differences in environmental resources will lead to divergence and speciation. We test this by using two different environmental conditions of bimodal and uniform random seed distributions. We also want to answer the question on the role of female mate preference in speciation. We use two different sexual selection methods, assortative and random mating, to help answer this question.

For each of these four possible configurations, we formed a corresponding hypothesis (H1–H4) as to whether or not we would find speciation:

H1 For random bimodal seeds and assortative sexual selection we expect to find speciation.

H2 For random bimodal seeds and random sexual selection we expect to find directional selection (no speciation).

H3 For random uniform seeds and assortative sexual selection we expect to find pseudo-speciation.

H4 For random uniform seeds and random sexual selection we do not expect to find speciation.

These four hypotheses are shown in Table 1.1.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	H1	H3
Random Mating	H2	H4

Table 1.1: Four hypotheses.

For random bimodal seeds and assortative sexual selection (H1) we were confident that speciation would occur resulting in two species. We reasoned that the bimodal seed distribution provides the environmental structure needed to support two species along with assortative selection which ensures that reproduction produces viable offspring.

We reasoned that both cases involving random sexual selection (H2 and H4) would result in a single population (no speciation). Offspring have a beak size based on the average of both parents, placing each new offspring near the center of the population. Any large differences in beak size will quickly be averaged out.

For random uniform seeds and assortative sexual selection (H3), there was no clear consensus on what the outcome would be. We reasoned that it would be similar to the case with bimodal seeds, but lacking the underlying structure.

CHAPTER 2

Related Work

In this dissertation our focus is on how behavior and different environmental conditions affect the development of sympatric speciation. In the past, artificial life and evolutionary computation researchers have placed artificial barriers in their environments in order to foster the development of diverse populations (multiple species) as discussed herein.

2.1 Fitness Landscape

One important abstraction we can use when describing the development of speciation is the concept of a fitness landscape. There are two distinct concepts of a fitness landscape in the literature. The first is the evolutionary biology fitness landscape and the second is the evolutionary computation fitness landscape. The former deals with internal or implicit fitness—that is, how frequently an organism reproduces in a given environment. If it reproduces frequently it has a high fitness and a low fitness if does not. The later deals with external or explicit fitness—that is, how well an individual matches with some external criteria relevant to the researcher employing the evolutionary computation method. If it matches well, it is deemed fit and given a greater probability of surviving and reproducing. Our work is clearly a case of the first kind of fitness lanscape, not the second.

If our systems find only a single maximum (whether local or global) each time they are run, there is a good chance each time that they will find the same species. If a single run finds multiple species, on the other hand, our chances of finding one or more distinct species goes up dramatically.

This increase is probably not simply a multiple of the number of species found, either.

That is, if we evolve ten species in a single run I think we are more likely to find unique strategies among those ten species than if we evolve one species each run for ten runs for a total of ten species. One simple reason for this is because we might well find the same (or a very similar) strategy on each of the 10 separate runs whereas with 10 species evolved in a single run, species will compete with each other, thereby pushing one another to find different strategies. This is particularly true if the global maximum in some environment is a given strategy and our evolutionary method is particularly good at finding the global maximum.

Another way to say this is that each approach to passing on genes could be seen as an evolutionary niche, in some sense. Since speciation is all about finding and exploiting niches, speciation is the natural way to find those different niches.

Further, different types of strategies may be more likely to evolve in environments that include other species. For example, protecting offspring from predators may be more likely to evolve in an environment that includes specialized predator species. Conversely, preying on other organisms to feed to your offspring may be more likely to evolve in an environment that includes potential prey species.

Another way to look at this issue is to see the presence of multiple species as providing a richness to the environment that wouldn't be present otherwise. This, in turn, can lead to more interesting strategies for exploiting that environment.

2.2 State Variable Models

State variable or equational models are commonly used in evolutionary biology for modeling sympatric speciation (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003). These models are useful in describing the mean-field aspects of a system in which large population sizes are assumed. Here, mean-field aspects of the system refer to the dynamics at the population level.

State variable models can become very complex when trying to model even simple behaviors which contain nonlinear effects, "...equational models are generally poor at dealing with the highly nonlinear affects such as thresholding, if-then-else conditionals, and so on that that often arise in biology..." (Carnahan et al., 1997). In our work we use both thresholding and conditional statements to model the behavior of our individuals.

The state variable approach has been applied to models of ground finches involving sympatric speciation (Martins et al., 2001).

2.3 Agent-Based Models

In order to reach our long term goal, we believe that agent-based models (Kampis and Gulyás, 2008), also known as individual-based (Grimm, 1999; Collins and Jefferson, 1994) or object-oriented models (Lorek and Sonnenschein, 1998) are essential. Agent-based models can handle non-linear effects without a large increase in complexity. On the other hand, state variable models can become very complex when trying to model even simple behaviors which contain nonlinear effects. Frameworks for building physics-based simulations are available from robotics researchers (Magnenat et al., 2009) which provide a suitable environment for ecological simulations.

There are many desirable attributes of individual-based models. "It is frequently more economical and transparent to describe such systems by organisms acting according to a few simple rules, their collective action giving rise to complex emergent behavior" (Carnahan et al., 1997). Transparency is important because we are not only motivated to build complex systems that parallel biological systems in richness and complexity, we are also interested in understanding the systems we build.

In addition, individual-based models may be useful in formulating general theories of ecology (Gras et al., 2009). It is possible that individual-based models can capture subtle interactions which may be necessary for different forms of speciation. "While analytic models typically describe only the equilibria of the model in question, microanalytic simulated evolution allows the exploration of the evolutionary dynamics of populations away from the equilibria" (Collins and Jefferson, 1994). Here, microanalytic refers to the low-level details of the system, details that individual-based modeling can handle.

Kampis and Gulyás (2008) identified the use of agent-based modeling as crucial to the development of complexity. The connection to our long-term research is clear, we would like to evolve different forms of behavior, both instinctive and those involving higher levels of complexity such as learning.

The development of efficient, full-featured ecology simulations is a time-consuming and error-prone task. Railsback (2001) calls for the increased collaboration between computer scientists and biologists for building simulation frameworks. In addition to a review of multi-agent systems and ecological management simulations, Bousquet and Le Page (2004) presents a historical perspective on the rich interdisciplinary interaction between biologists and computer scientists and also calls for the strengthening of this interaction. It also identifies the key role that computer science plays in the future development of ecological multi-agent simulations.

2.4 Speciation

In most evolutionary computation and artificial life studies there is a single population, within which either all members freely interbreed (typically using a recombination operator known as crossover) or none of which interbreed (typically variation here is introduced through different types of mutation) (De Jong, 2006; Bedau, 2003). In nature, by contrast, there are countless populations within which there is significant interbreeding yet between which there is little or no breeding. These populations are often known as *species* and the division of a single interbreeding population into multiple distinct such populations is known as *speciation*. Species may provide a wealth of diversity in an environment by filling distinct niches.

Additional artificial mechanisms could be used to subdivide the population more or less completely, and many such mechanisms have been proposed including crowding (De Jong, 1975), niching (Goldberg, 1989; Horn et al., 1994), tagging (Spears, 1994), imposing a population topology (Sarma, 1998), and using islands (Whitley et al., 1999). All of these approaches have merits for their intended applications but are not entirely appropriate for ours. In particular, none of them allow for new niches to arise based on the behaviors (e.g., resource use) of groups within the population.

Rather than impose upon the algorithm population divisions, or additional mechanisms to promote population divisions (Gras et al., 2009), we would prefer to allow speciation to occur based on interactions between individuals within an environment where the interactions arise from mechanisms and actions inherently necessary for the individual's survival and procreation.

2.5 Artificial Life

The artificial life community is interested in understanding how certain biological processes such as speciation can also create new and diverse forms of artificial life (Langton, 1989). Researchers are interested in the grand challenge of open-ended evolution (Ray, 1993; Adami and Brown, 1994), and a better understanding of natural phenomenon (Collins and Jefferson, 1994).

Yaeger (1994) created an ecological simulator inspired by Braitenberg (1986); Walter (1951), among others. Although he was initially interested in "the neural evolution of architectures for systems faced with complex behavioral tasks" he expanded his model to include behavioral and reproductive processes. He found that, by placing physical barriers in the environment, he could encourage the development of multiple species with different behaviors. This is an important feature that promoted the emergence of speciation in his work.

We too were initially motivated by the evolution of neural architectures for different behavioral tasks, but it became apparent that speciation was missing from most research related to neural evolution. In particular, the research in this area is mostly focused on evolving individuals performing tasks in isolation from one another.

We identified cooperation and competition as one of the key elements that we want to explore in the context of multi-agent systems. In particular, we want to explore parent-child relationships in robots and how speciation could lead to the evolution of learning.

A recent example of artificial life research is Gras et al. (2009) who studied speciation and mate selection behavior in a predator-prey model. Of particular interest, they evolved the behavior the individuals using a fuzzy cognative map. In their work, they explicitly encoded the concept of a species using a cluster model based on a genomic distance metric. In our work we use the female mate preference to implicitly form the clusters in a more natural way.

In addition, this community is interested in understanding how speciation can lead to the development of higher-level behavior. Gracias et al. (1997) who extended the work of Yaeger (1994), found "a deep connection between the complexity of behaviors emerged and the difficulties posed by the world." This implies that speciation alone is not sufficient to guarantee the development of higher level behavior (Kampis and Gulyás, 2008). I believe that in addition to speciation a diverse environment is needed to evolve learning (Chalmers, 1990).

Early researchers were aware of the importance of sexual selection and its application to artificial life. "Sexual selection through mate choice was overlooked in biology for over a hundred years following Darwin (1871). The evolutionary computation community need not repeat the same mistake" (Miller, 1994).

Biologists have identified behavior as another cause for speciation, in particular female mate preference (Seehausen and van Alphen, 1999; Seehausen et al., 1997). Over the last decade there has been considerable work that provides support for behavior being an important factor on sympatric speciation (Coyne and Orr, 2004). Assortative mating behavior has been identified as a key element in the development of sympatric speciation (Seehausen and van Alphen, 1999). It is believed that female mating behavior helps to create virtual barriers between sub-species or varieties.

For example, in the Galapagos islands, small populations of birds with different beak sizes (species) are known to inhabit the islands. If allopatric speciation was the only type of speciation it could be assumed that each island would contain a different species of it own. Surprisingly, each island contains multiple species living and breeding on it.

By using sympatric speciation, artificial life researchers can support a rich diversity of artificial lifeforms without the need for physical barriers. Adding assortative mating to agent-based simulations allows for the natural emergence of speciation and hence diversification. “This common feature suggests that the evolution of biodiversity may be driven not simply by natural-selective adaptation to ecological niches, but by subtle interactions between natural selection and sexual selection” (Todd and Miller, 1997).

Maley (1998) identifies requirements for modeling species diversity. “A model to examine species diversity grounded in our knowledge of microevolutionary dynamics must include representations of organisms, species, geography, and the dynamics of sexual reproduction, mutation, migration, death, and predation.” The ecological system on which we are basing our simulation, the Galapagos finches, does not contain a strong migration component (although it is true that some birds are known to move from island to island). Also, there are owls which are known predators of ground finches on the Galapagos islands. We do not address the general topic of predation, but it has been used in other simulations involving sympatric speciation (Gras et al., 2009).

Kampis and Gulyas (2004) observed the emergence of multiple species by the introduction of new phenotype dimensions (multiple phenotypic traits). In this dissertation a single phenotypic trait will be used to avoid the complexity of dealing with multiple traits. In their work, they used a constrained energy-system—imposing a natural limit on the number of individuals that can be supported. In this dissertation the number of individuals is also constrained, the population size is related directly to the number of seeds available.

Maley (1998) identifies the need to validate artificial life simulations with established ecological and evolutionary theory. Experimental data is hard to acquire in general. In our case, the finch data collected by the Grants on the Galapagos island is available, but we have used principles from evolutionary biology to validate our process and to justify some of the simplifications made in the design of our experiments. Validation with actual finch data is of interest to us and is left as future work.

2.6 Evolutionary Computation

The evolutionary computation community can also benefit from sympatric speciation. Speciation can be viewed in some sense as a search through a fitness landscape. Evolutionary computation methods, such as genetic algorithms, typically search this space using a single population of individuals which converge (through the loss of diversity) on a single region in parameter space. “Evolutionary algorithms often suffer from premature loss of population diversity which limits their adaptive capabilities and possible application to hard problems like multi-modal and multi-objective optimization” (Drezewski and Siwik, 2006). Evolutionary algorithms could benefit from the application of speciation and sexual selection, “However these mechanisms are not widely used as a way of maintaining useful genetic diversity in evolutionary algorithms” (Dreżewski and Siwik, 2008). Current research does explore the use of multiple populations but, typically, this process involves the explicit creation of the structure needed to represent multiple populations (Graham and Oppacher, 2007). The use of sympatric speciation can automate this process creating new populations to explore the various niches as needed like multi-objective evolutionary algorithms (Deb, 2001).

One recent example of research in the evolutionary computation community is Ebner et al. (2010), who found spontaneous sympatric speciation by initiating an arms race through co-evolving entities. This arms race causes the penotypic landscape to be explored using multiple species. One interesting aspect of this work is that the fitness for each individual was interdependent, “each species deforms the fitness landscape and thereby interacts with other species located nearby.”

Another example of interdependent fitness is Huang (2003) who studied mate selection in the context of genetic algorithms. Huang found that, through this approach, the population was able to “retain genetic diversity, and better utilize building blocks already discovered for exploration of the search space.”

Another example of applying sympatric speciation to evolutionary computation is Drezewski and Siwik (2006), in which sexual selection is applied to multi-objective optimization. Eppstein et al. (2006), a collaboration between computer scientists and a biologist, demonstrated sympatric speciation using a patched-based system without the use of mate selection, although the species were slow to emerge.

2.7 Rapid Speciation

Darwin (1859) believed that, in general, evolution is something that takes place over the millennia—far too slow to observe in his own lifetime. What researchers have found is that a combination of high variability, extreme natural selection and intense sexual selection can lead to accelerated speciation. Finding examples of rapid speciation in nature can be useful for biologists in quantifying the process of evolution over a period of tens of years instead of thousands or millions of years.

The application of rapid speciation can also be useful to artificial life researchers. Although computational power is increasing at an exponential rate, rapid speciation can allow simulations to run faster on current computational hardware.

2.8 Open-ended Evolution

Researchers from both evolutionary computation (Drezewski and Siwik, 2006) and artificial life (Ray, 1993; Kampis and Gulyas, 2004; Chaumont et al., 2007) have identified open-ended evolution as a motivation for their work. Sympatric speciation supports this goal by maintaining population diversity. “Ultimately, we believe that systems capable of displaying nearly open-ended evolution of complex morphologies and behaviors should be used to study basic questions in evolutionary biology that cannot be addressed by any other means, such as the mode and manner of speciation via niche speciation, its relation to mate selection, and the emergence of ecologies” (Chaumont et al., 2007).

2.9 Simulation

Gathering data in the field is a time-consuming, labor intensive process. The datasets gathered are typically incomplete. Simulations allow biologists to run experiments that would be otherwise “impossible, impractical, or unethical to perform on biological organisms and communities” (Chaumont et al., 2007).

Simulations are an important research tool for biologists for validating their theories. “Computer simulations of the behavior of virtual populations, immersed in well-defined habitats and evolving under a representation of the dynamics of evolution, have generated a wealth of reliable data with which to test our models and the assumptions they rely on” (Martins et al., 2001).

2.10 Open Questions

The definition of a species is an open question (Sherratt and Wilkinson, 2009). Our working definition of species follows the (widely accepted) biological species concept (Mayr, 1963), two or more interbreeding populations of individuals that are reproductively isolated. Mayer also proposed an additional constraint—complete speciation is irreversible—once established, species are incapable of merging back together. Gras et al. (2009) opposes this view and thus leaves open the possibility of fusion. Kampis et al. (2007) identified 22 species concepts/definitions from the literature. Using an agent-based environment they found that “different species measures tend to yield similar or identical classifications if there is enough time for natural selection to operate."

How do we identify a species in agent-based/object-oriented simulations? In many equational models it is assumed that you have two or more predefined populations. In agent-based models such as ours, the formation of species is an emergent property of the system. For analysis of the evolutionary dynamics, a way is needed to identify the different species. Yaeger (1994) also identified the need to quantify the different species found in his simulations.

In our work, we used visual inspection to analyze our *phenophylogenetic* trees (defined below), but we are interested in automating the process which will allow us to better identify the population dynamics. Others have used methods based on fuzzy sets to build a phylogenetic tree (Clement, 2006). The most appealing answer to us an automated clustering algorithm which could be used to build a more abstract tree representation.

How do you visualize the phylogenetic tree? An important part of our research was how to best visualize the phenotypic information. Gras et al. (2009) also identifies the need to visualize the phylogenetic tree of their species. Visualization is an important tool for validating the framework and in understanding the large amounts of data collected during our simulation runs.

We found in addition to the phylogenetic information (who is related to who) it is useful to plot the beak/seed size along the x-axis. The result is a pseudo-density plot which we call a *phenophylogenetic* tree. It is particularly appealing to us given the tight genotype/phenotype coupling (the genotype and phenotype are the same throughout our experiments) along with the fact that we are using a single locus in our genome.

What is the effect of small populations on the evolutionary process? Recent evidence shows a direct link to rising temperatures due to climate change and the disruption of ecological habitats for plants (log) and animals (Beever et al., 2011). It is likely that increasing restrictions on native habitats will lead to smaller population sizes for many species.

CHAPTER 3

Methodology

This section outlines the basic setup we will use to perform our experiments and provides insight as to why we chose one method over another for modeling different processes such as natural selection and sexual selection. In some cases we used a simpler-is-better approach, however in all cases we used insight gained from what is known from the finch studies on the Galapagos Islands.

3.1 Overview

The speciation experiment is a simulation of evolving a population with multiple species. Here, the evolutionary process is modeled as natural selection followed by sexual selection. Natural selection removes individuals from the population while sexual selection along with reproduction adds new offspring. Natural selection and sexual selection work together to change a population over time. In order to maintain stability in the evolutionary process as a whole (avoiding boom-crash cycles) there must be a balance between natural selection and sexual selection.

Life on the island is modeled by an extended period of natural selection followed by sexual selection and reproduction. Natural selection lasts for a fixed number of days and applies a selective pressure from the environment. At the start of natural selection, the island is full of seeds virtually guaranteeing that each individual will find food. As the selection event wears on, more and more individuals will perish due to the dwindling supply of seeds. Note that no individuals are born during the natural selection period.

Sexual selection takes place after natural selection. In sexual selection, the females do the choosing by selecting a mate based on their own individual preference. Different types of female preference are possible. In all cases, the preference is based on beak size. In assortative mating, the female picks a male which has a beak size similar to her own. In our model this is mimicked by females prefering a male with the largest beak size. Finally in random mating the female exercises no preference.

After the female selects a male an offspring is produced and enters the population. The beak size for the new individual is the average of the mother and father plus a small amount of variation. The gender of the offspring is random, maintaining a 50/50 sex ratio.

3.2 Simulation Model

Careful consideration was given to amount of detail added to the simulation. The modus operandi for this work was to favor a simpler simulation without adding unnecessary complexity. When trying to understand a complex process I believe it is best to remove any features that are not absolutely necessary.

For this work, certain relationships between various parameters are important. It was important to model the yearly cycle with a sufficient length (number of days). Choosing 100 days verses say 200 is a good tradeoff between the length of the dry season and the number of seeds at the beginning of the dry season. More seeds requires more computational time for the simulation and results in longer runs. The slowdown occurs because searching for seeds inside a bounded region is in the critical path of the code. See Chapter 4 for a detailed description of the system architecture.

The average energy available for a given seed is independent of the seed size because it is assumed that the body size is proportional to the beak size. In the Galapagos islands, some of the ground finches are known to vary only in their beak size from species to species. In our simulations, we wanted to avoid a bias toward birds with larger beak sizes. In nature there are multiple forces that work to balance the distribution of different species, including the interplay between sexual selection, natural selection, and the developmental process. In effect, an individual gains no advantage by having a larger beak other than access to larger seeds and females with larger beaks.

We put considerable effort into the stabilization of the population size. We found that the clutch size was an important factor in controlling the growth of the population. The clutch size combined with the lifespan of the individuals determines the total number of offspring the females will produce in a given year. Producing too many offspring can lead to a booming population followed by extinction.

3.3 Feeding Behavior

The feeding behavior for each individual is greedy non-altruistic. Consequently, an individual with an energy close to the maximum will still consume a seed, possibly utilizing only a small amount of energy contained therein. In an alternate approach the individual only consumes the energy it needs leaving the remaining energy for later consumption. This is an interesting approach and worth investigating in our simulations.

Given the previous discussion on non-altruistic feeding behavior, it is clear that the population will rapidly exhaust the supply of seeds if not regulated in some way. By limiting the search area for seeds on the island, we in effect limit the rate of consumption without causing mass extinction for the entire population.

The feeding behavior can be modeled as a probabilistic sampling method. Different sampling methods include Gaussian, triangular, and uniform. We chose the uniform sampling method because of it's simplicity but we are also interested in investigating other methods. The other two methods will clearly smooth out the edges of the feeding range but it is unclear what effect they will have on the dynamics of the system.

3.4 Mating Behavior

Mating behavior can also be modeled as a probabilistic sampling method. We chose to use the same sampling method for mating as we did for feeding. In this case the individual (the female in our case) is selecting another individual (a male) based on their beak size. We chose uniform selection because it was the simplest method in terms of function and ease of implementation and it supports the assortative mating behavior. The uniform sampling method is attractive because by varying the width of the window, the choosiness of a female can vary from very selective to purely random.

CHAPTER 4

System Architecture

The system architecture describes the overall structure of a system. A good system architecture incorporates certain design philosophies such as encapsulation which decouple different components of the system. In an object-oriented language these components are coded as a collection of classes.

4.1 Classes

The system is based on a top level SpeciationExperiment object along with a set of loosely-coupled message passing objects. The class relationships between the different components of the system are shown in Figure 4.1. Each class is a well defined model of some aspect of the natural system.

Here, the solid lines represents an association between between classes, in particular, which classes belong to other classes. For example, the Island class has a Configuration, Seeds and Individuals classes. Each class may include a number representing the multiplicity of the association, where the '*' character represents an unlimited number of objects. For example, there could be multiple Seed objects associated with each Seeds container. The dashed lines represent a dependency between two classes where one class acts as a supplier for another class. In this architecture, the TwisterRandom class supplies all the other classes with random numbers.

It is interesting to observe that the Seed class is not directly connected to the TwisterRandom class. This is because the Seed class is static (the seed size and location do not change in the simulation) and therefore it does not require a source of randomness. On the other hand, the Individual class is dynamic and thus requires a source of randomness. For example, a female (an instance of the Individual class) needs a source of randomness to select mates and produce offspring.

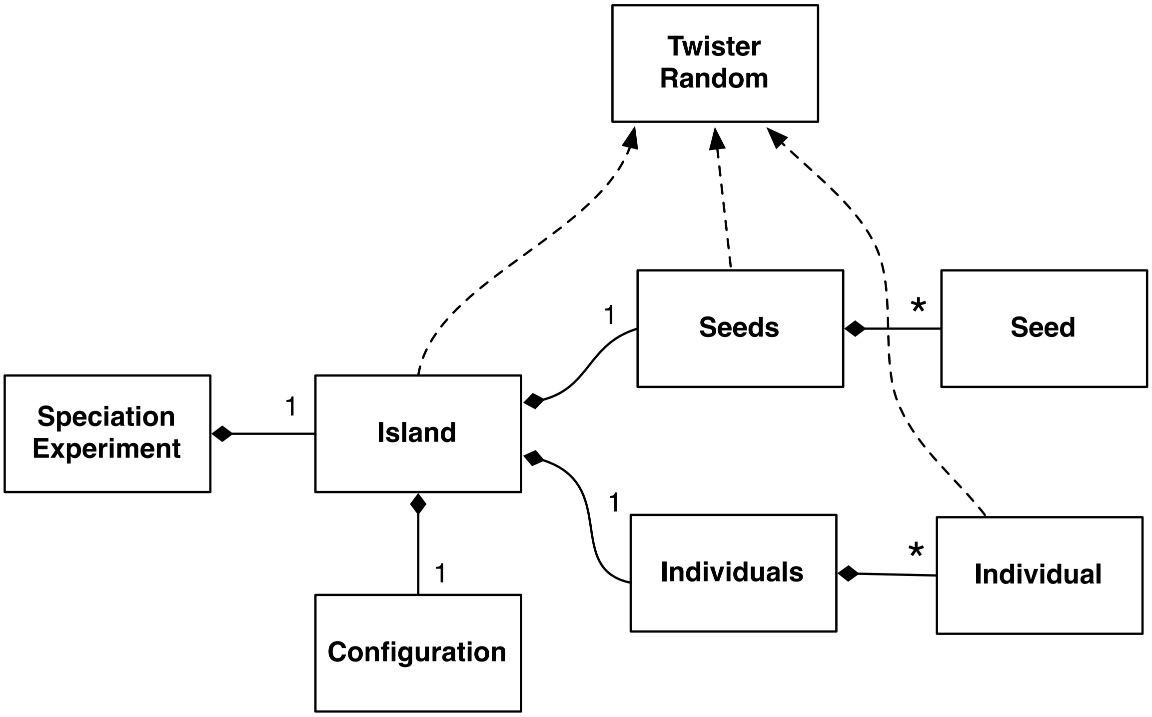

Figure 4.1: The class relationships between the different components of the system.

4.1.1 Speciation Experiment

The SpeciationExperiment class is the top level class. The SpeciationExperiment class also contains the main() function which creates a SpeciationExperiment object. It contains methods for setting the run directory and configuration file paths and a process for creating and initializing the Island object. After initialization is complete, this object starts the simulation by sending an appropriate message to the Island object.

4.1.2 Configuration

The Configuration class holds the configuration (a table, in the form of key-value pairs) for the experimental run. It contains a method which loads the configuration file. Various configuration parameters are accessed through methods which include error checking to ensure that the key exists in the dictionary.

4.1.3 Island

The Island class contains properties describing the physical size of an island, along with the seeds and individuals it contains. State information is maintained such as the current day and generation index. The Island class contains a run method that provides the entry point into the simulation.

The run method loads the configuration file into the configuration object. The run method creates the run directory and places a copy of the configuration file in this directory for future reference. The run method creates the initial population using the specified number of individuals and distribution. More specifically an Individuals object is created and Individual objects are added to this container. The run method sets up a log file.

4.1.4 Seed

The Seed class models the location, size, and energy of a seed along with a comparison method useful for sorting seeds by size.

4.1.5 Seeds

The Seeds class acts as a container for Seed objects. It supplies methods for adding and removing seeds individually. It also supplies methods for operating on multiple seeds at once. Iterating internally inside a class is more efficient since it has low level access to the underlying data structure. Therefore, methods for adding multiple seeds at once, finding seeds within a given size range or spatial region, sorting seeds, and writing the seeds to a file are provided.

4.1.6 TwisterRandom

The TwisterRandom class provides support for random number generation. A source of high quality random numbers is needed throughout the architecture, in particular the creation of the Individual and Seed objects. Performance is also a concern along with the need to have a single source for all randomness in the simulation. A means of setting the random number generator to a known state is provided to aid in such tasks as initialization and unit testing. Support for integer and floating point primitives, including uniform and Gaussian distributions, is provided.

4.1.7 Individual

The Individual class models all aspects of an individual including the age, beak size, energy, gender, and location. It also provides a means of uniquely identifying an individual and its parents. It includes methods for accessing and changing these properties. It also includes class methods for the generation of unique identifiers. The overall approach in this architecture is individual-centric and therefore this class provides methods for interaction with the island. These methods include searching for food and finding a mate.

4.1.8 Individuals

The Individuals class acts as a container for Individual objects. It supplies methods for adding and removing a single individual. It also supplies methods for operating on multiple individuals at once. Iterating internally inside a class is more efficient since it has low level access to the underlying data structure. Therefore, methods for adding multiple individuals at once, searching for individuals based on beak size, energy level, gender, and mating count, are provided. Methods for shuffling and sorting a population are provided along with methods for writing the population to a file. Fast iteration during natural and sexual selection is important and therefore methods are provided for this purpose.

CHAPTER 5

Experimental Procedure

The experimental procedure is designed to capture the main aspects of life for a finch population on one of the Galapagos islands. A yearly/seasonal cycle on the island includes an extended dry season followed by a wet season in which mating and reproduction take place.

The experimental procedure contains three important parts, natural selection, sexual selection, and reproduction. Natural selection is an interval with a fixed number of days in which food becomes more and more scarce. During each day of natural selection, each individual in the population is allowed to search for and consume food. During sexual selection each female is allowed to select a male to mate with and produce offspring. Restrictions are placed on the individuals in the population including maximum lifetime and the number of times individuals can mate.

5.1 Initial Population

The island contains an initial population of 400 individuals with random beak sizes (Gaussian, mean 5.5, variance 0.5) and randomly determined 50:50 sex ratio. The energy level of each individual is set to zero and the age is set to one. The initial population distribution is the same for all four experimental conditions.

5.2 Before Natural Selection

Before we begin natural selection, the mating count for each individual is reset to zero. The mating count is used to limit the number of times a male can mate in any given year. Any seeds remaining from the previous year are removed and new seeds are added to the island.

5.3 Natural Selection

Natural selection lasts for a period of 100 days. On each day, the individuals search the island looking for seeds. As each day passes there are fewer and fewer seeds on the island—simulating an extended dry season found in the Galapagos islands.

5.4 Each Day of Natural Selection

On each day of natural selection, each individual in the population is allowed one feeding attempt—the order is random. This single feeding attempt can be thought of the average energy consumed by an individual during each day.

To find a seed, an individual first picks a random region of the island to search. This region is a square region 10 units on each side and located randomly within the extents of the island. The island is 100 x 100 units in size. Second, the individual looks for seeds within the random region. Acceptable seeds are seeds that are within the individual's beak size range—e.g. plus or minus one unit from the beak size. For example, an individual with a beak size of 4.2 can only select seeds within the range 3.2 to 5.2. The individual selects a random seed from the acceptable seeds, the individual's energy level is increased, on average, by one unit and the seed is removed from the island. The exact amount of energy contained in any given seed varies randomly from zero to two units of energy (uniformly random). Variability was added to the energy amount in order to stabilize the evolutionary dynamics—that is, to avoid synchronous population extinction.

There is a cost associated with searching and finding seeds. To account for this, after feeding, the individual's energy level is decreased by 0.1 units of energy. Note that the energy level is decreased even if no seed is consumed. Here the important constraint is that the energy gained (on average) is much more than the cost for finding a seed.

After accounting for the cost for searching, the energy level of the individual is examined. If the energy level of an individual falls below zero, it is removed from the population.

Each individual is able to store up to two units of energy. Thus, an individual can survive without food for twenty days after consuming two seeds containing at least one unit of energy.

At the end of each day, the number of individuals in the population is checked. If there are fewer than two individuals in the population the simulation ends.

5.5 Sexual Selection

During sexual selection all females are allowed to select a male and produce offspring. In this simulation, the female embodies two possible mating behaviors—assortative mating and random mating.

5.6 Assortative Mating

For assortative mating, the female is picky with respect to the male she chooses. First, the female determines which males are within her beak size range. If there is more than one acceptable male, the female randomly chooses one of the males. To limit the influence of a single male, and to account for the limited energy males have for courting females, males are only allowed to mate five times per year.

5.7 Random Mating

In random mating a female selects one of the males in the population randomly (without preference to beak size). Males are restricted, as in the assortative mating case, to mating a maximum of five times per year. Note that assortative mating degenerates into random mating if the acceptable beak size range is made large enough to encompass all males for any given female.

5.8 Reproduction

The female mates with the selected male and produces offspring if her energy level is positive. The offspring is produced with a beak size that is the average of the mother and father's beak size plus a small amount of random mutation/variation (Gaussian, mean 0, variance 0.2). The gender of the new offspring is determined randomly and the offspring's age and energy level are set to zero. The new offspring is added to the population.

5.9 After Reproduction

After sexual selection the age of each individual in the population is incremented by one and the elders (individuals older than 4 years) are removed. The size of the population is checked. The simulation is stopped if there are fewer than two individuals left.

CHAPTER 6

Results

The data was comprised of 48 repetitions for each of the four experimental conditions Bimodal Seeds and Assortative Mating (BSAM), Bimodal Seeds and Random Mating (BSRM), Uniform Seeds and Assortative Mating (USAM), and Uniform Seeds and Random Mating, for up to 1000 generations. A repetition can end before 1000 generations if complete extinction occurs. In each run (a particular repetition) we logged information related to the individuals and the seeds which resulted in over a million data files totaling approximately 40,000,000,000 bytes. The data recorded for each individual included energy, beak size, age, gender, mating count, a unique identifier and the identifiers of its parents. The data recorded for each seed includes energy and location. The graphs show each individual in the population, plotted with respect to beak size (horizontal axis) and year (vertical axis) with lines connecting parents to offspring. This gives a visual representation of the data that allows us to look for speciation over time. The tables present snapshots of cumulative data such as the average number of populations for each experimental condition at the end of the simulation repetitions.

6.1 Population Graphs

The basic layout of the population graphs is given as follows. Two different colors are used to represent the individuals who survived natural selection (blue/dark) and those who perished (green/light). A marker is drawn for all the individuals in a given generation. The individuals who perished during natural selection are superimposed on the individuals who survived natural selection. Females are represented as circles, males are squares. In

Figure 6.1, for example, a male (ID #258) present in the first generation has a beak size of 7.15, lives for four generations, and dies.

We connect each individual to its parents using lines. These lines are more visible in repetitions with a smaller number of generations. In Figure 6.2, for example, a male with a beak size of 4.06 (ID #411) is born in the third generation, has a mother (ID #401), born in the second generation, with a beak size of 3.91 and a father (ID #138), born in the first generation, with a beak size of 4.35.

Note that the beak size of an individual is not just the average of its parents. Mutation is added to the blended value and can result in high variability. In Figure 6.1 for example, a female (ID #409) with a beak size of 6.24 is born in the third generation who dies during natural selection. This female has a beak size much smaller than either of her parents.

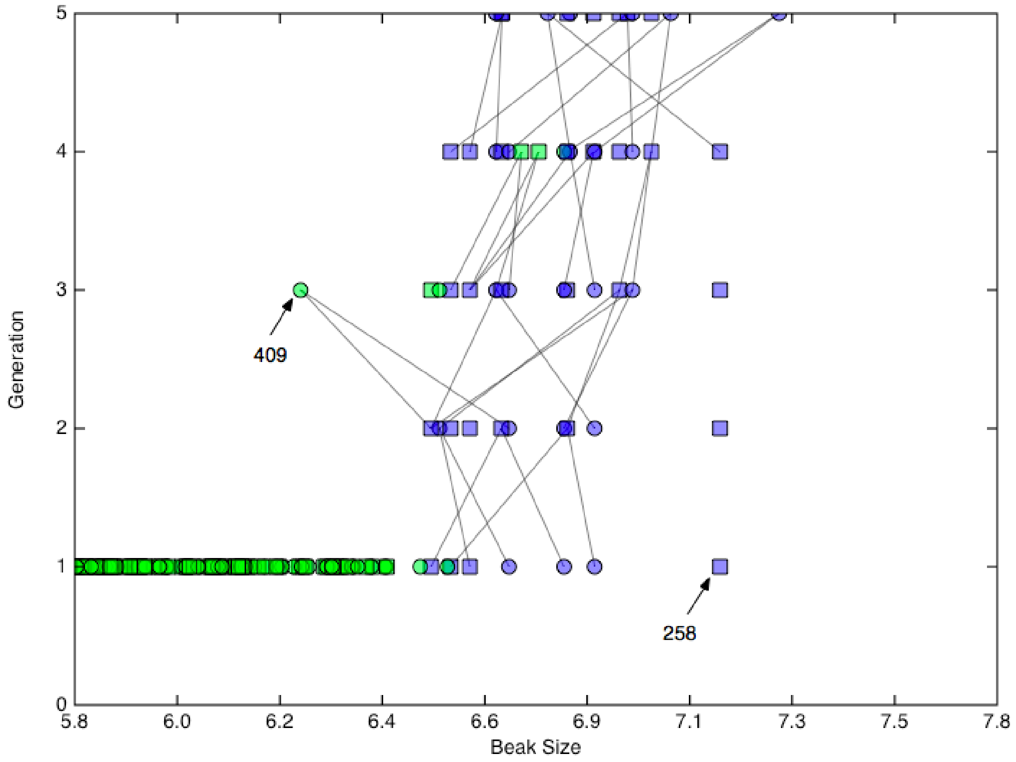

Figure 6.1: BSAM, Generations 1–10, Run 1. An example of a population graph. Right Branch.

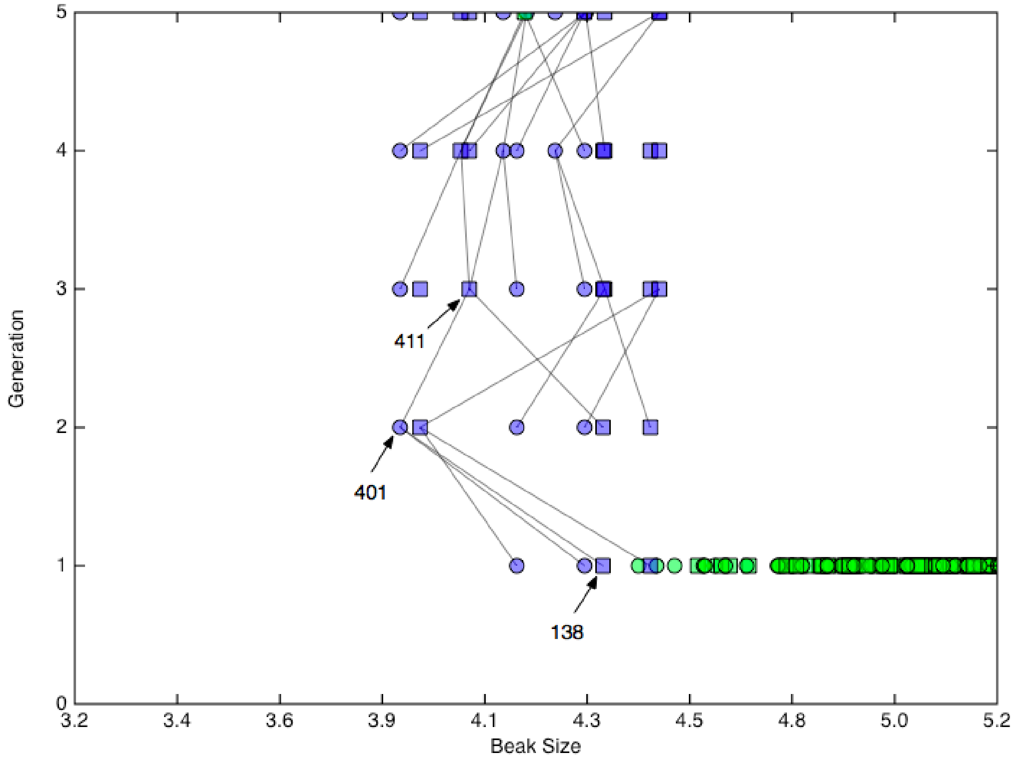

Figure 6.2: BSAM, Generations 1–10, Run 1. An example of a population graph. Left Branch.

6.2 1x Seeds

The section includes the results for the BSAM, BSRM, USAM, and USRM configurations for the case when there are 5000 (1x) seeds. Population graphs are shown along with quantitative results detailing the average population size, the number of populaitons found, and extinction events.

6.2.1 Bimodal Seeds & Assortative Mating

The results for BSAM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for BSAM Run 1 are shown in Figure 6.3 as a prototypical example. There is a large die-off of the initial population as illustrated by the wide green/light horizontal bar in the first generation. In each repetition a large proportion of the population died with only the individuals at the tails of the original population surviving natural selection.

Two non-interbreeding populations are present—there are no lines between the left and right branches. As a result, no hybrid offspring with intermediate beak sizes are produced. The individuals born near the inner edge of each branch have a higher mortality rate than those who are born on the outer edge of each branch.

In seven repetitions (Run 4, 17, 22, 31, 37, 40, and 45) the left branch went extinct. See Run 4 (Figure 6.4) for a representative example. In 6 repetitions (Run 3, 5, 10, 19, 26, and 44) the right branch went extinct. See Run 3 (Figure 6.5) for a representative example. In the remaining 35 repetitions both branches remained stable up to generation 10, i.e., there were no complete extinctions. See Run 2 (Figure 6.6) for a representative example.

In most of the repetitions in which one of the branches went extinct, it went extinct because the associated population contained only males. In 11 repetitions (Run 3, 4, 5,

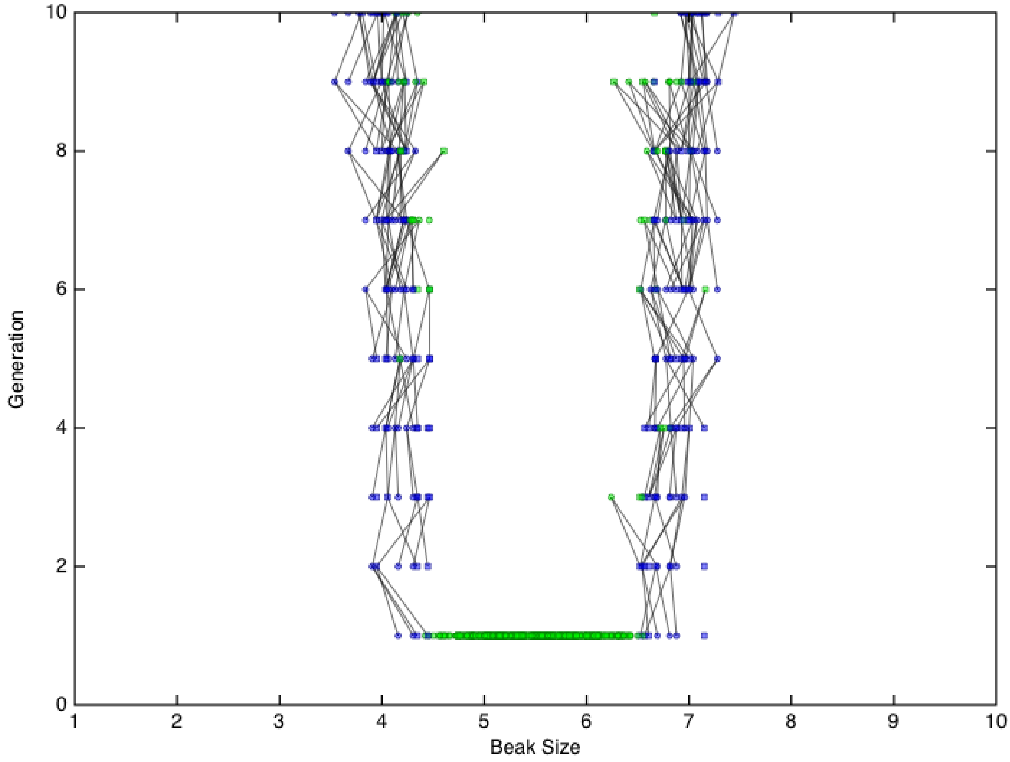

Figure 6.3: BSAM, Generations 1–10, Run 1. A prototypical example of a population with two non-interbreeding branches.

17, 22, 26, 31, 37,40, 44, 45) one of the branches went extinct due to the lack of females. See Figure 6.4 for a representative example. In only two repetitions (Run 10, 19) the population went extinct due to a lack of males in the population. See Run 19 (Figure 6.7) for a representative example.

In eight repetitions (Run 4, 5, 10, 19, 22, 26, 44, 45) one of the branches underwent rapid extinction due to the lack of reproduction in the initial population. See Figure 6.4 for a representative example. In five repetitions (Run 3, 17, 31, 37, 40) one of the branches underwent gradual (non-rapid) extinction due to limited reproduction in the initial population. See Figure 6.5 for a representative example. Complete extinction of both branches did not occur within the first 10 generations.

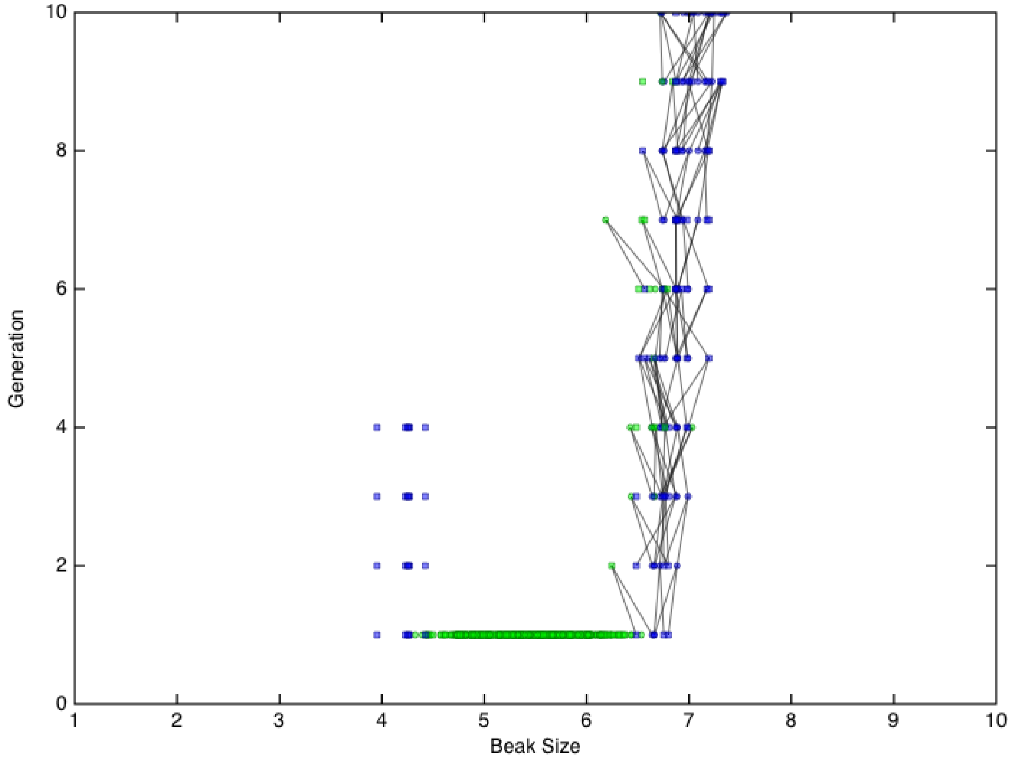

Figure 6.4: BSAM, Generations 1–10, Run 4. A representative example of left branch rapid extinction due to the lack of females.

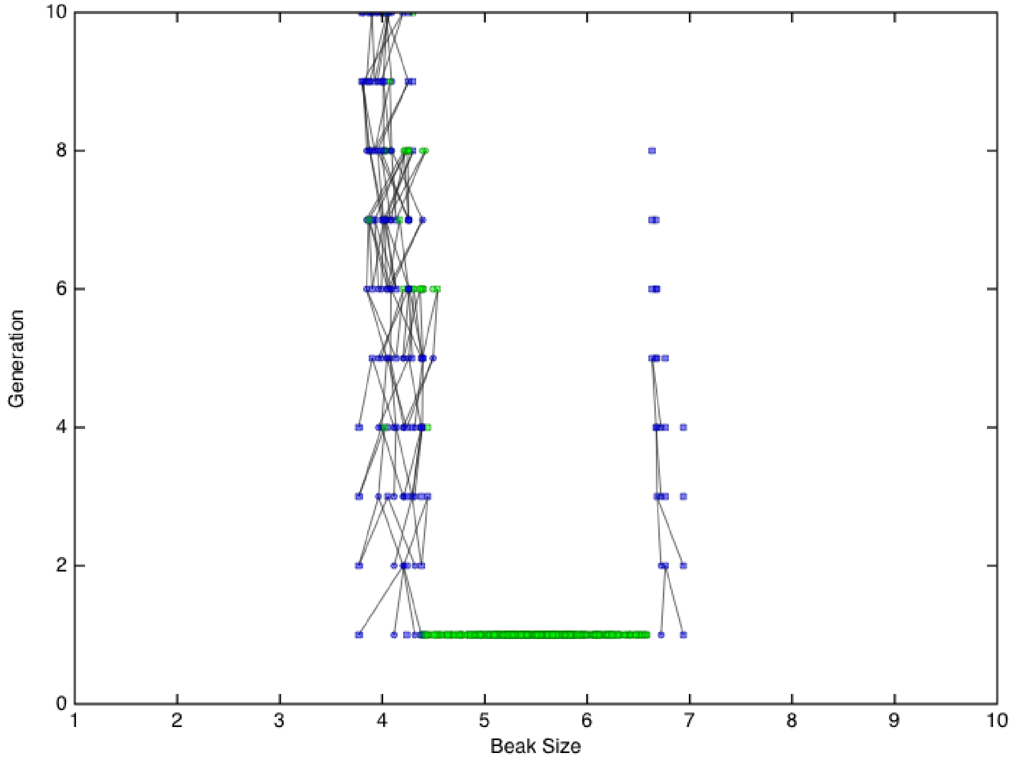

Figure 6.5: BSAM, Generations 1–10, Run 3. A representative example of gradual right branch extinction due to limited reproduction.

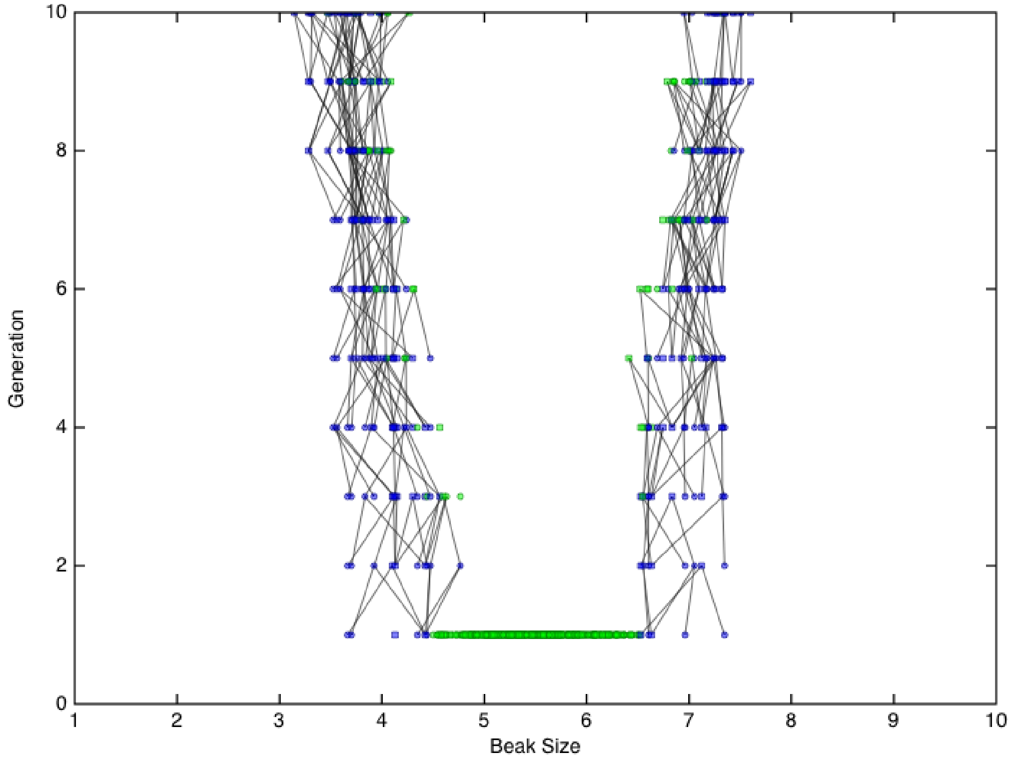

Figure 6.6: BSAM, Generations 1–10, Run 2. A representative example of a population where both branches remained stable up to generation 10.

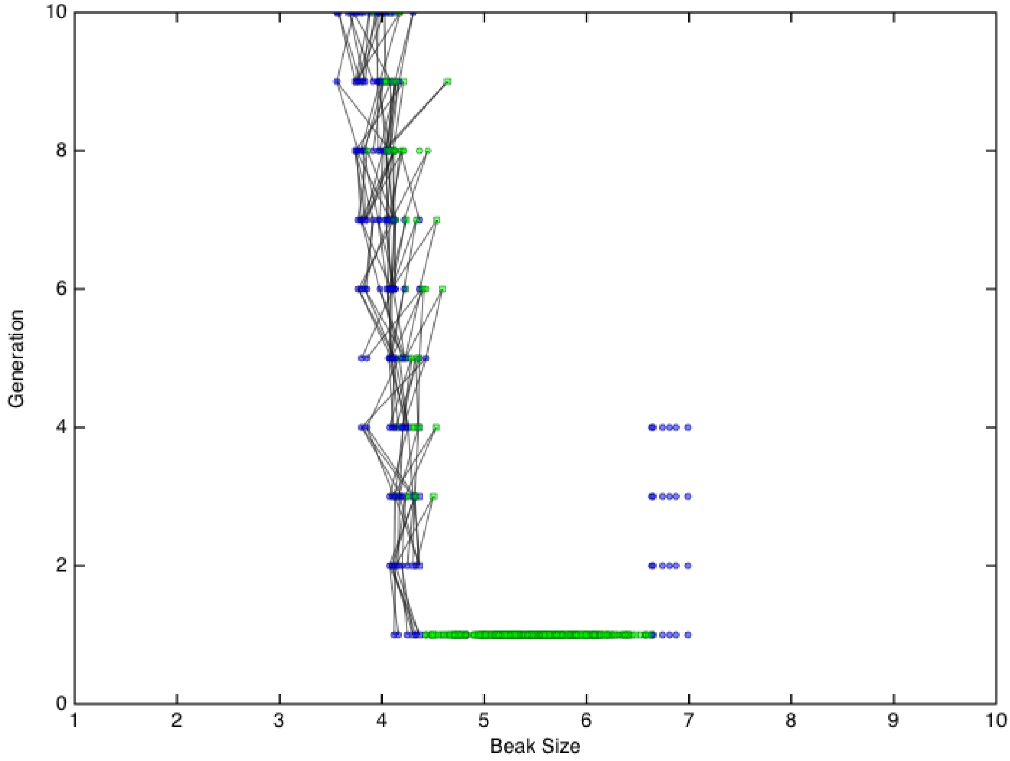

Figure 6.7: BSAM, Generations 1–10, Run 19. A representative example of (right) branch extinction due to a lack of males.

Generation 1–100 Plots

The first 100 generations for BSAM Run 1 are shown in Figure 6.8 as a prototypical example. There are two populations in the first generation after natural selection, with approximate beak sizes of four and seven. The left and right branches form a "U" shape—two roughly symmetric curves which approach beak sizes of three and eight by generation forty. During this interval the width (variance) of each population appears to widen as the simulation approaches generation 40. After generation 40, the average beak size and variance of each population remains about the same.

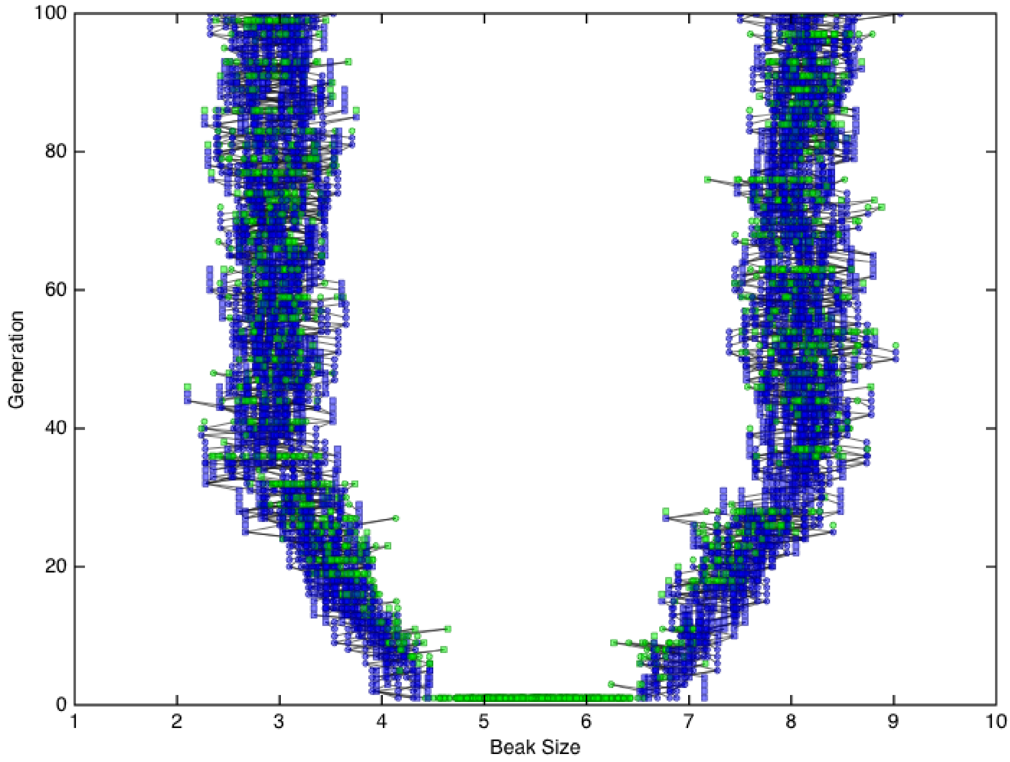

Figure 6.8: BSAM, Generation 1–100, Run 1. A prototypical example of two roughly symmetric branches forming a "U" shape.

It is clear that more individuals, around generation ten, are dying off during natural selection along the inner edge of each branch, and more individuals are surviving natural selection along the outer edge of each branch. It appears that this concentrated die-off becomes more diffuse by generation thirty. Also, repeated green/light horizontal bars are present in the left and right branches indicating large-scale periodic die-offs of the given subpopulation.

There were a number of exceptional repetitions. In Run 30 (Figure 6.9), the left branch was highly variable around generation 30. In three repitiions (Run 18, 20, and 42) one of the branches is skewed. A representative example is shown in Figure 6.10. The right branch in this figure remains somewhat stationary for the first 20 generations and then rapidly shifts to a larger average beak size. Also note that this branch has a large number of green/light offspring along the left edge of the curve indicating a large die-off.

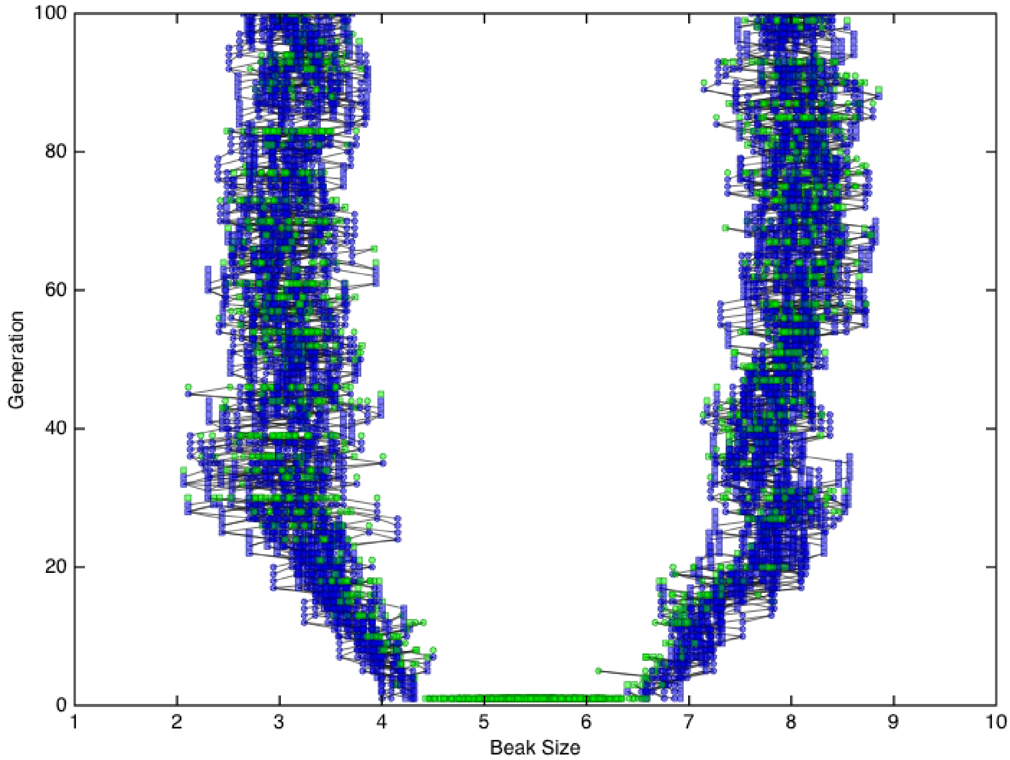

Figure 6.9: BSAM, Generation 1–100, Run 30. An example of a highly variable branch (left, around generation 30).

Branch extinction after generation 10 and before generation 100 is a rare event. In a single repetition, Run 13 (Figure 6.11), the right branch went extinct well before generation

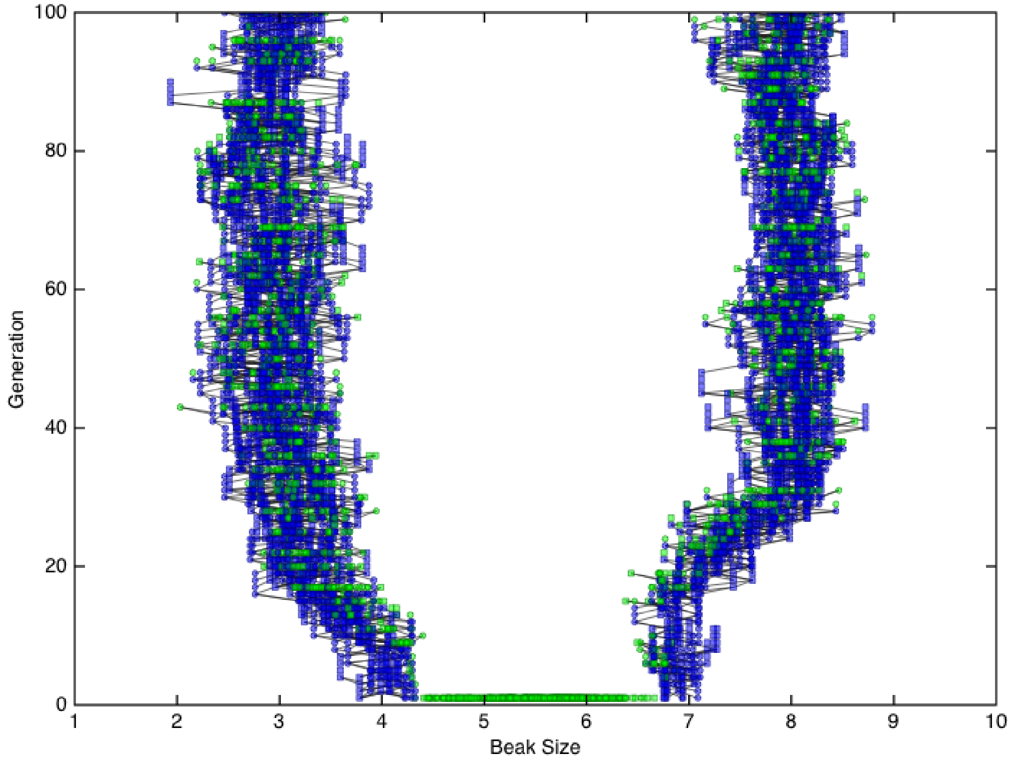

Figure 6.10: BSAM, Generation 1–100, Run 42. A representative example of a skewed (right) branch.

100 due to a lack of females. Interestingly, complete extinction, the extinction of both branches, did not occur after generation 10 and before generation 100.

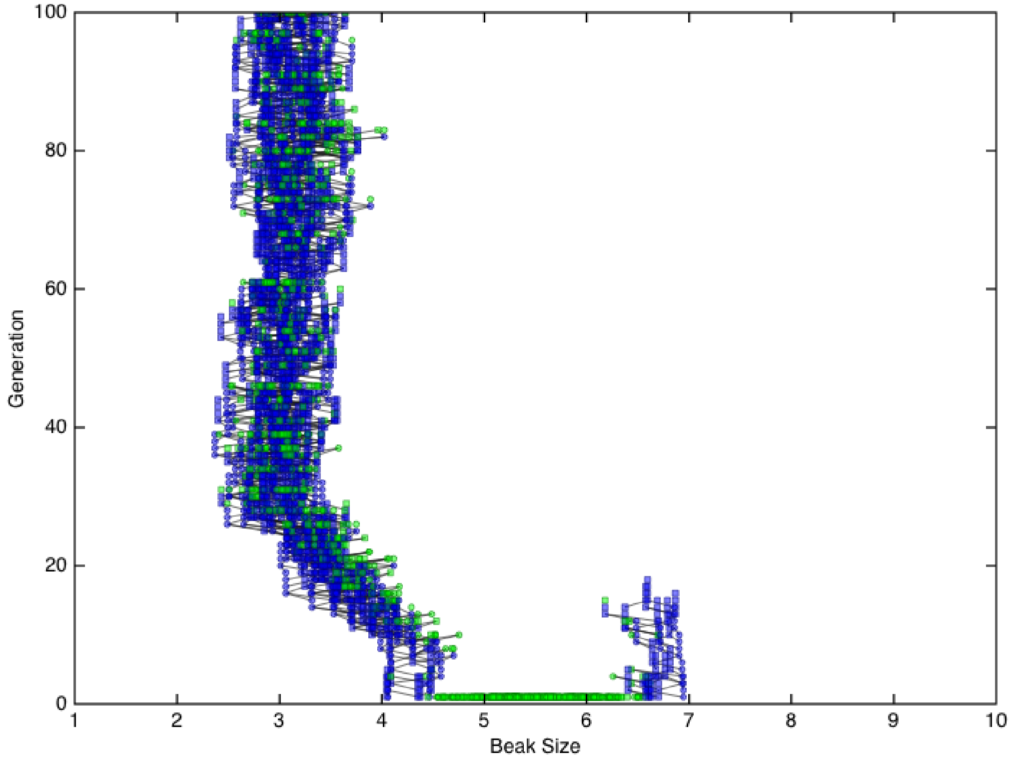

Figure 6.11: BSAM, Generation 1–100, Run 13. The single example of branch extinction after generation 10 and before generation 100.

Generation 1–1000 Plots

The first 1000 generations for BSAM Run 1 are shown in 6.12 as a prototypical example. It is clear that no interbreeding takes place between the two branches. The populations for the left and right branches have an average beak size of three and eight and remain stable up to 1000 generations. Stability here refers to the fact that the populations do not go extinct. The high amount of variability in the individuals is clearly visible.

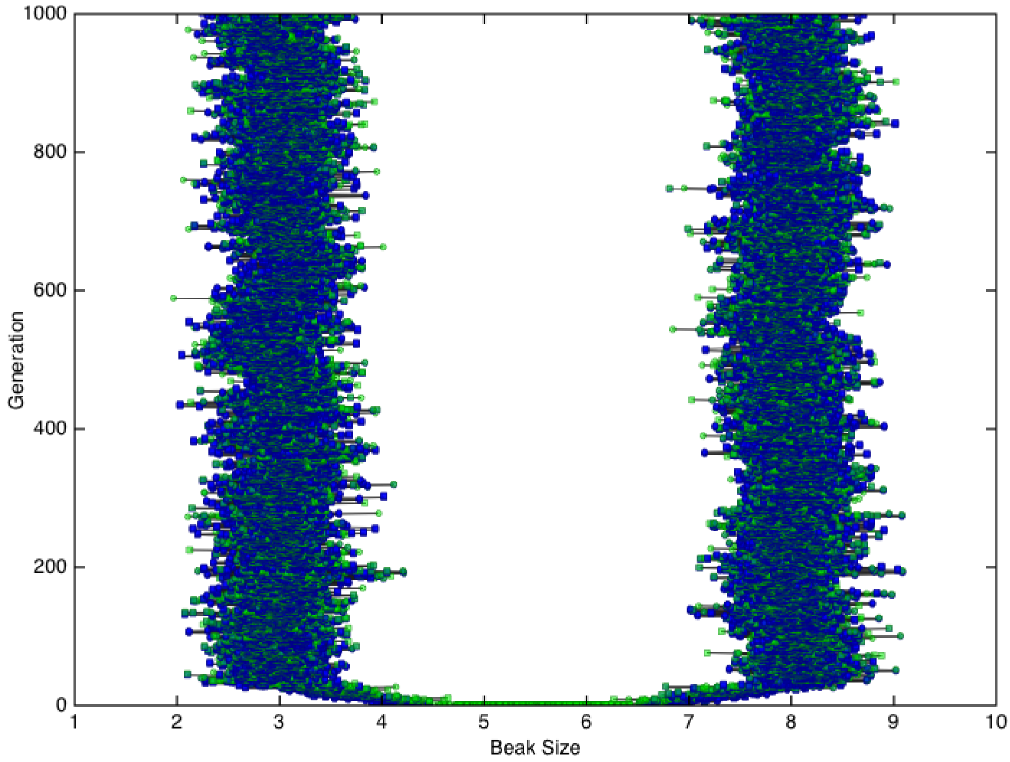

Figure 6.12: BSAM, Generation 1–1000, Run 1. A prototypical example of a population with two species present in the last generation.

Branch extinction after generation 100 and before generation 1000 is a rare event. In Run 36 (Figure 6.13) the left branch went extinct after generation 246 due to a lack of females. In Run 38 (Figure 6.14) the left branch went extinct after generation 285 due to a lack of males. This is one of the few cases where a lack of males led to extinction.

In 31 out of 48 repetitions, two species were present in the last generation. See Fig-

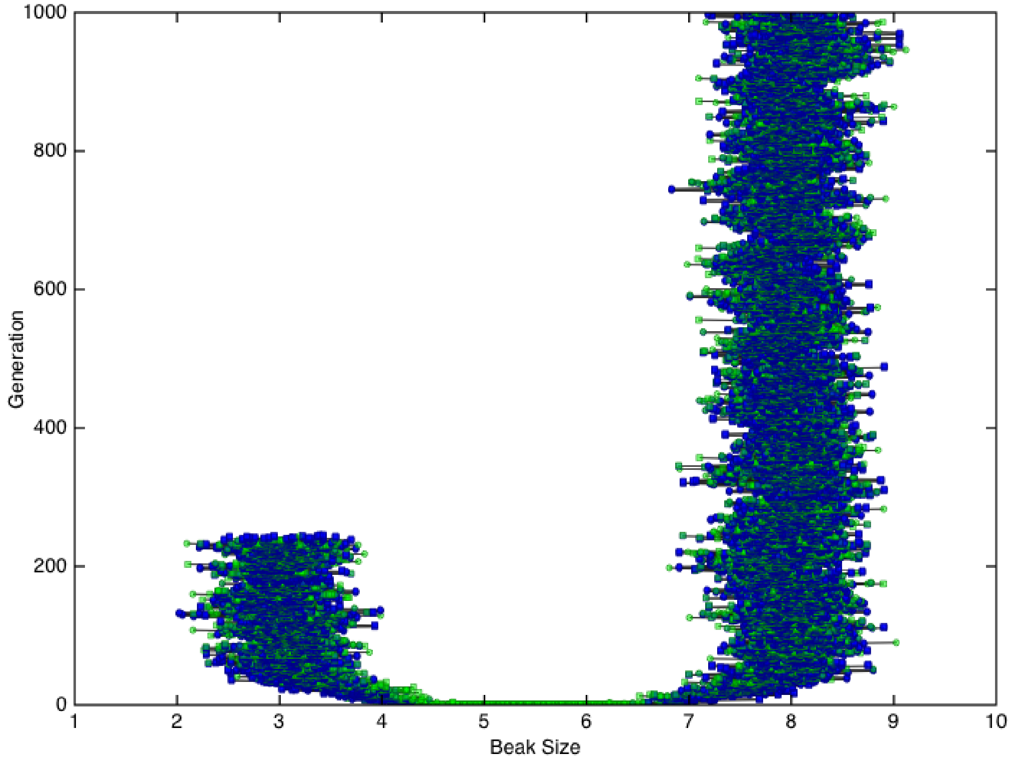

Figure 6.13: BSAM, Generation 1–1000, Run 36. A representative example of branch extinction due to the lack of females after generation 100 and before generation 1000.

ure 6.12 for a representative example. In 17 out of 48 repetitions, one of the two populations went extinct. See Figure 6.15 for a representative example. Complete extinction did not occur in any of the repetitions.

In Run 22, shown in Figure 6.16, there appears to be a dramatic shift in the average beak size for the right branch just before generation 400.

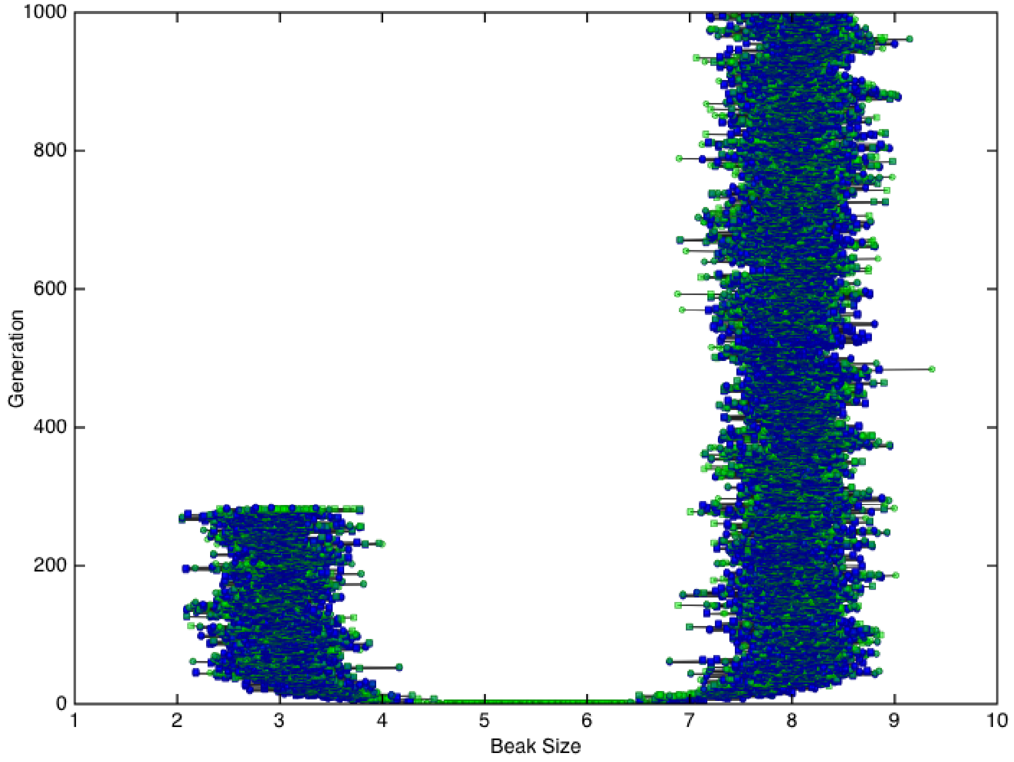

Figure 6.14: BSAM, Generation 1–1000, Run 38. A representative example of branch extinction due to the lack of males after generation 100 and before generation 1000.

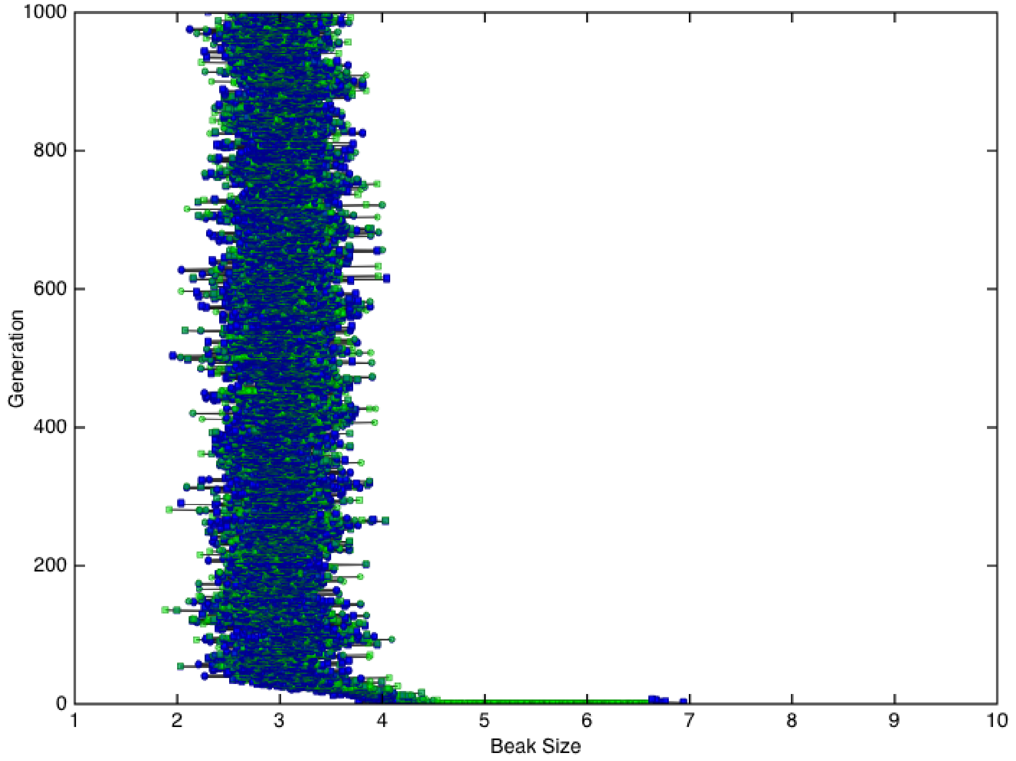

Figure 6.15: BSAM, Generation 1–1000, Run 3. A representative example of a population where one of the two branches went extinct.

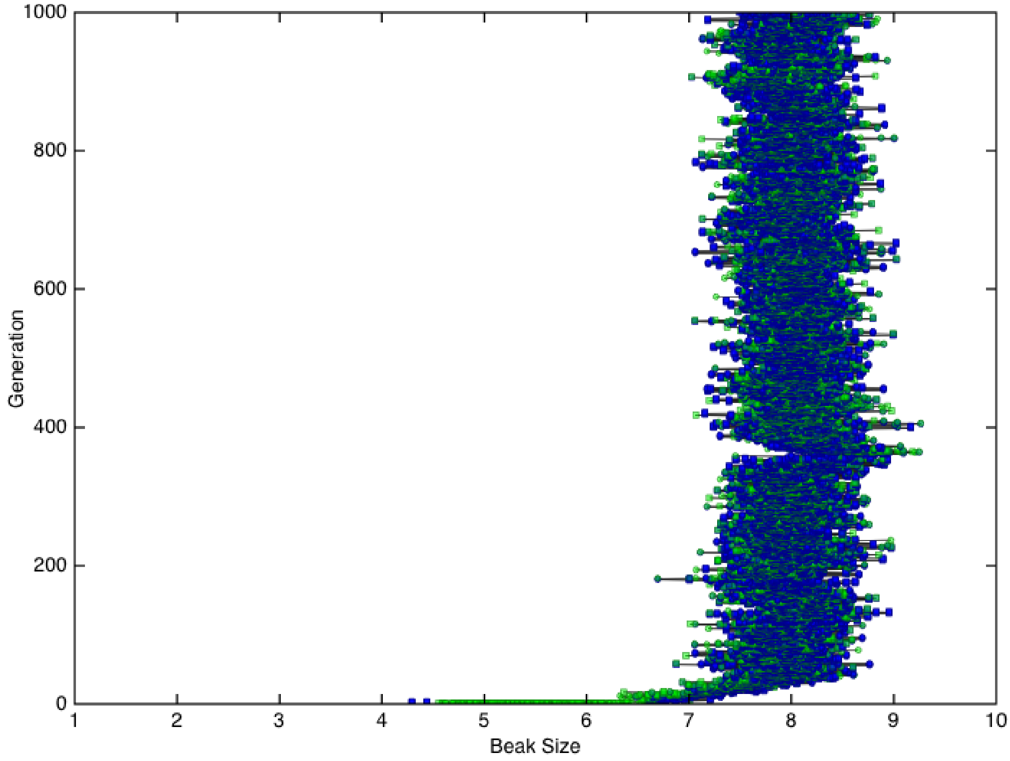

Figure 6.16: BSAM, Generation 1–1000, Run 22. An example of a dramatic shift in the average beak size for a branch.

6.2.2 Bimodal Seeds & Random Mating

The results for BSRM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for BSRM Run 1 are shown in Figure 6.17 as a prototypical example. The same large-scale die-off seen in the BSAM case is present in the first generation. One important difference is the large number of inviable (green/light) offspring which are born with intermediate beak sizes. The population as a whole is attempting to repopulate the intermediate beak/seed niche but the lack of intermediate sized seeds is causing the new offspring to perish due to natural selection. This is because, in random mating a female from one branch is just as likely to pick a male from the other branch, resulting in a child with an intermediate beak size. The prior argument is based on the assumption that there are equal numbers of males in both branches. It appears that the females in the left branch are gradually choosing more males from their own branch while the females in the right branch are gradually selecting more males from the opposite branch. It is because of this bias toward picking males in the left branch that the right branch goes extinct in generation nine.

In 15 repetitions (Run 2, 4, 8, 12, 14, 15, 16, 17, 20, 27, 28, 36, 39, 42, 44) the left branch went extinct. See Figure 6.18 for a representative example. In 14 repetitions (Run 1, 3, 5, 9, 13, 22, 30, 32, 33, 37, 38, 45, 46, 48) the right branch went extinct. See Figure 6.17 for a representative example. In three repetitions (Run 10, 21, 34) both branches went extinct. See Run 10 (Figure 6.19) for a representative example of complete extinction.

In 5 repetitions (Run 2, 5, 12, 27, 46) one of the branches underwent rapid extinction. Rapid extinction is the lack of successful reproduction in the initial population—no viable offspring are added to the branch. See Run 2 (Figure 6.20) for a representative example. In 25 repetitions, (Run 1, 3, 4, 8, 9, 13, 14, 15, 16, 17, 20, 22, 28, 30, 32, 33, 36, 37, 38, 39, 42, 44, 45, 48) one of the branches underwent gradual extinction. See Run 1 (Figure 6.17)

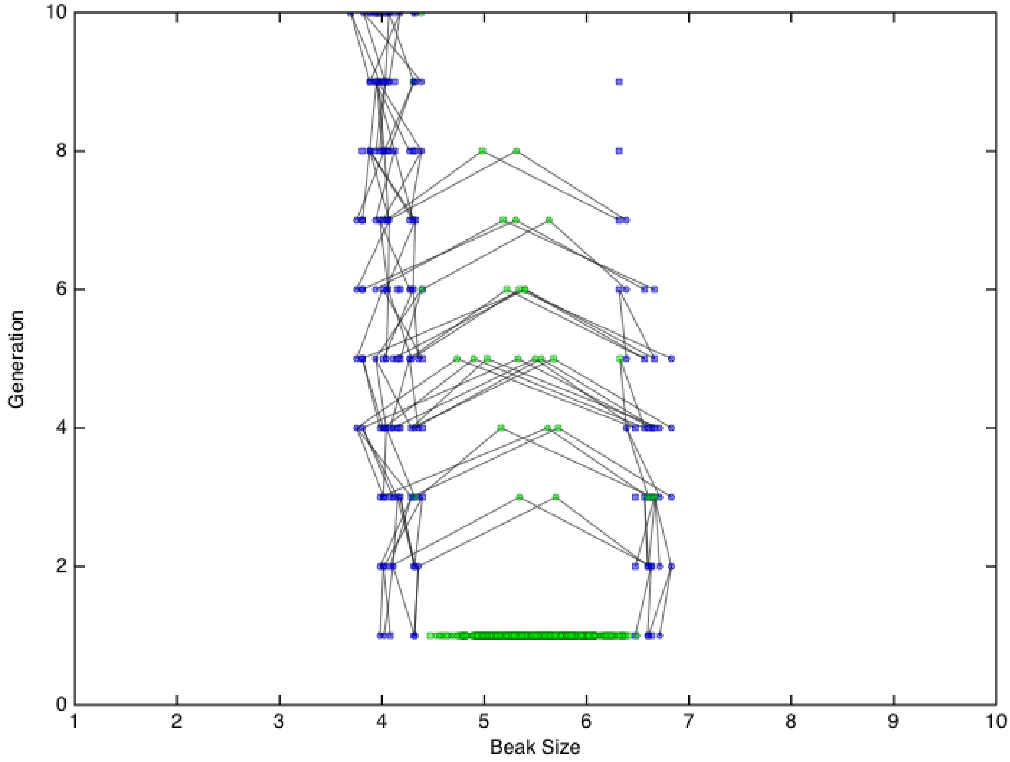

Figure 6.17: BSRM, Generation 1–10, Run 1. A prototypical example of a population supporting a single branch due to the gradual extinction of the other branch.

for a representative example.

Complete extinction can result from rapid or gradual extinction. In one repetition, Run 21 (Figure 6.21), the population underwent rapid extinction due to an initial population containing a single female in the left branch who by chance did not select a single male from her own population. In two repetitions (Run 10 and 34) the population underwent gradual extinction. See Run 10 (Figure 6.19) for a representative example.

In the remaining 16 repetitions both branches remained stable up to generation 10. See Figure 6.22 for a representative example.

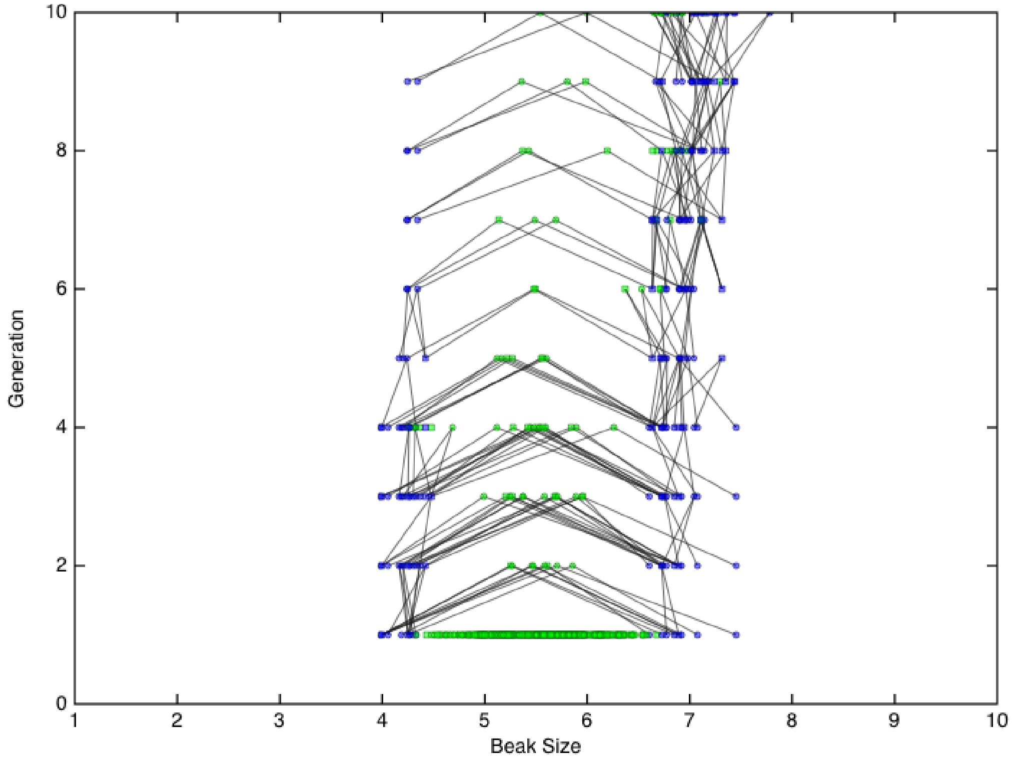

Figure 6.18: BSRM, Generation 1–10, Run 8. A representative example of gradual left branch extinction.

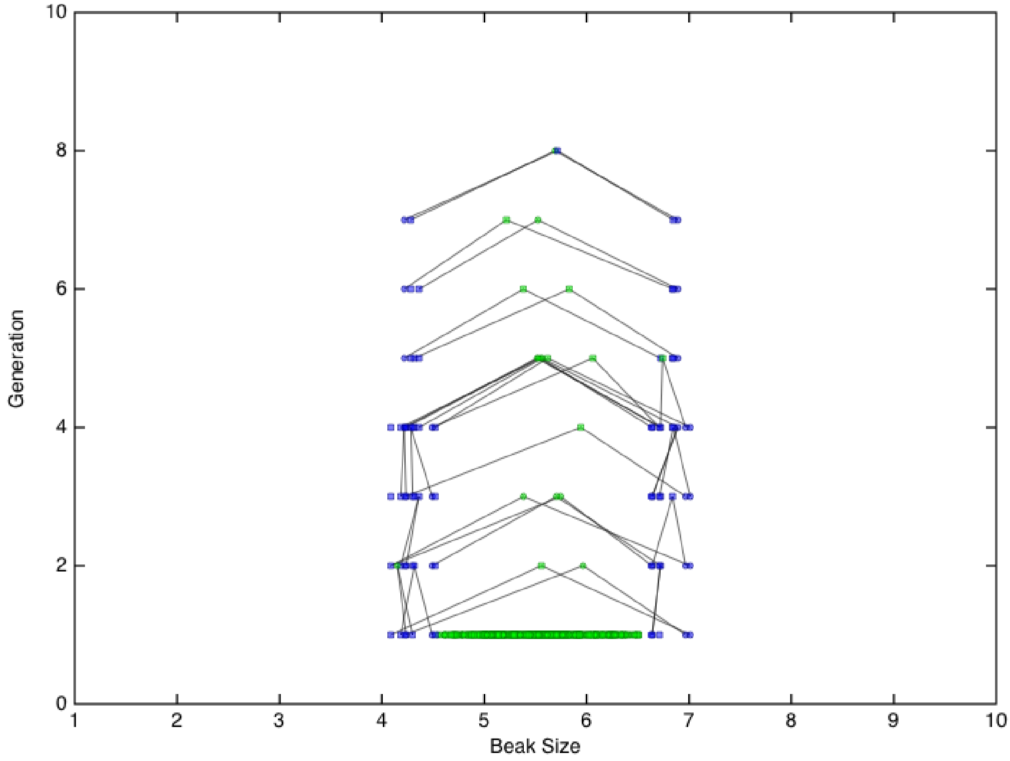

Figure 6.19: BSRM, Generation 1–10, Run 10. A representative example of gradual complete extinction.

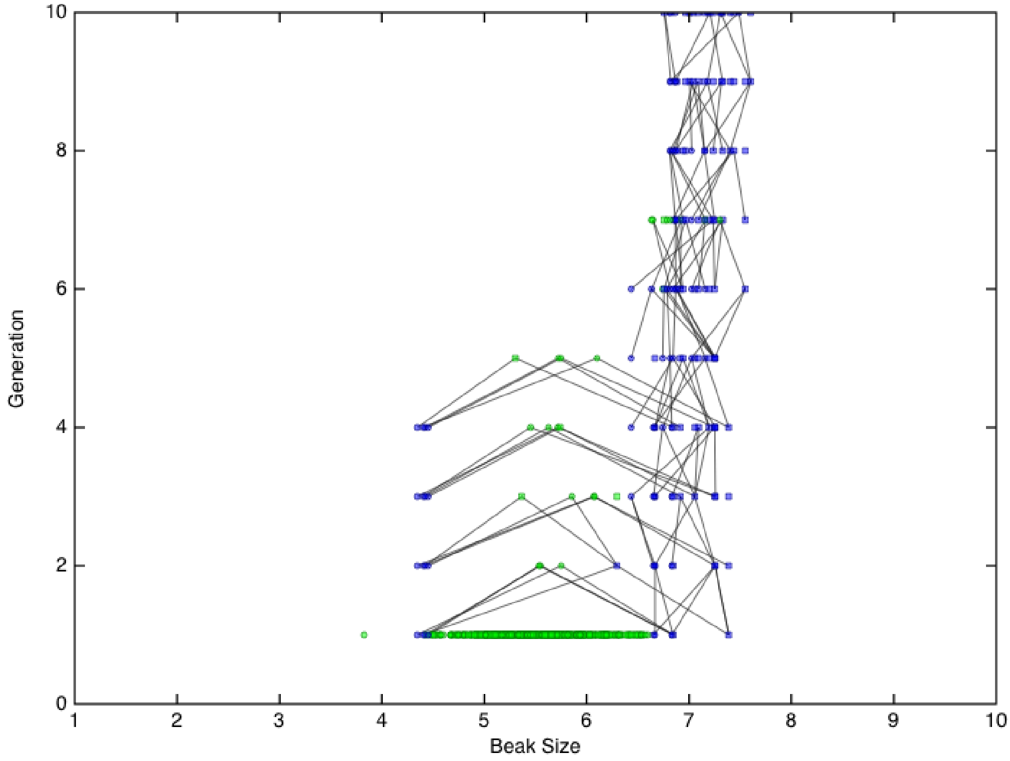

Figure 6.20: BSRM, Generation 1–10, Run 2. A representative example of (left) branch rapid extinction.

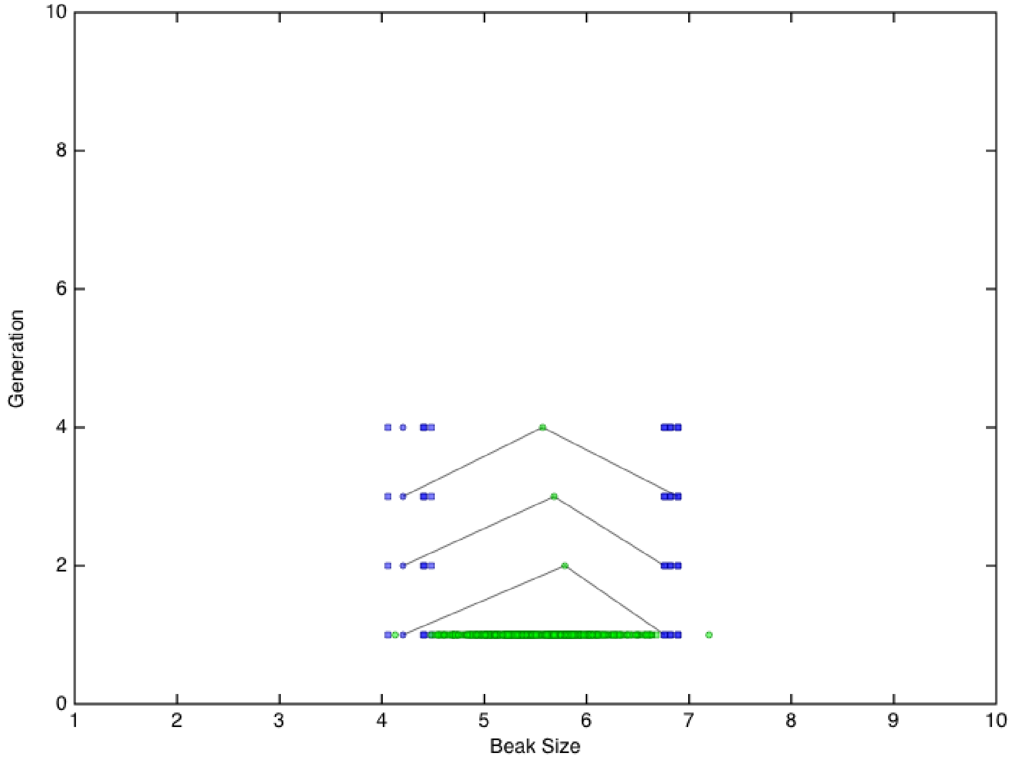

Figure 6.21: BSRM, Generation 1–10, Run 21. A representative example of complete rapid extinction.

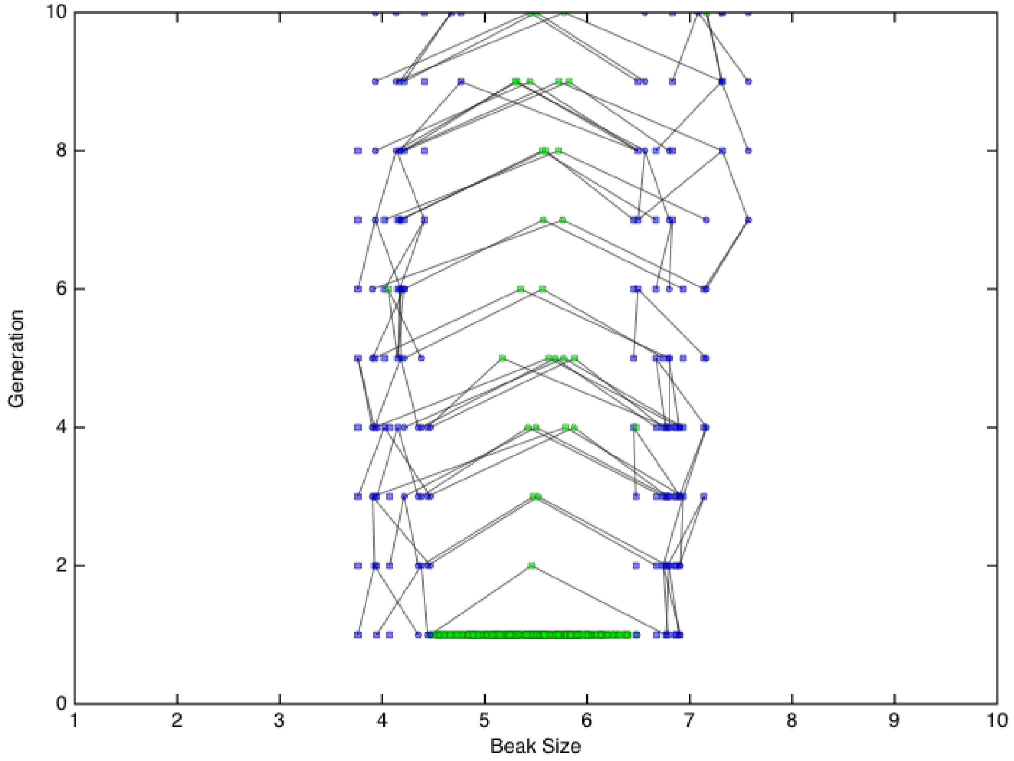

Figure 6.22: BSRM, Generation 1–10, Run 7. A representative example of a population where both branches remained stable.

Generation 1–100 Plots

The first 100 generations for BSRM Run 1 are shown in Figure 6.23 as a prototypical example. By generation 20, and in some cases much sooner, there was at most one branch stable up to generation 100. Around this time the production of inviable offspring also ceases. The shape of the stable branches, those that did not go extinct, is similar to the "U" shape seen for the BSAM configuration.

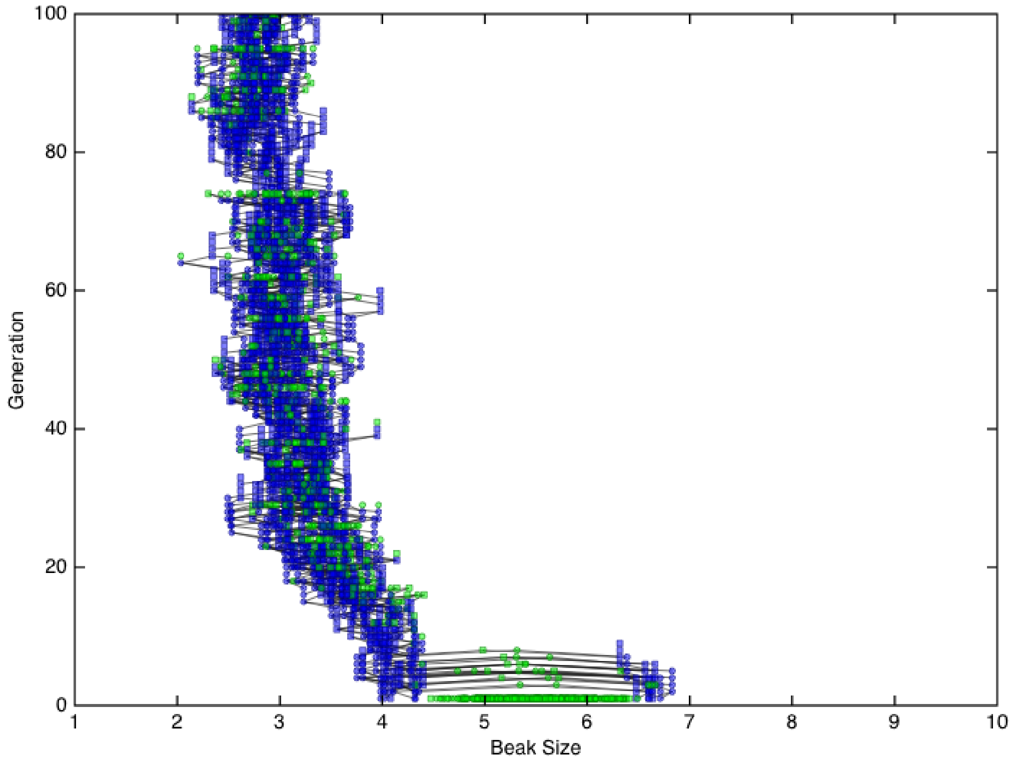

Figure 6.23: BSRM, Generation 1–100, Run 1. A prototypical example of a population supporting a single branch.

Again, as was the case for BSAM, the individuals near the inner edge of a branch are more likely to perish during natural selection compared to the individuals at the outer edge. Green/light banding, clearly visible near the inner edge of the branch, is indicative of this process. In this case, the effect is delayed five to ten generations.

Green/light horizontal bars, similar to those seen for BSAM, are present. For example, in Run 1 (Figure 6.23), a significant die-off occurs just after generation 70.

Overall, there are a number of extinctions after generation 10 and before generation 100. In eight repetitions (Run 7, 11, 23, 24, 29, 41, 43, and 47) only the left brach went extinct. See Figure 6.24 for a representative example. In six repetitions (18, 19, 25, 31, 35, and 40) only the right branch went extinct. See Figure 6.25 for a representative example. In a single repetition, Run 26 (Figure 6.26), both branches went extinct after generation 10 and before generation 100. It appears that both populations went extinct due to a lack of males in each population.

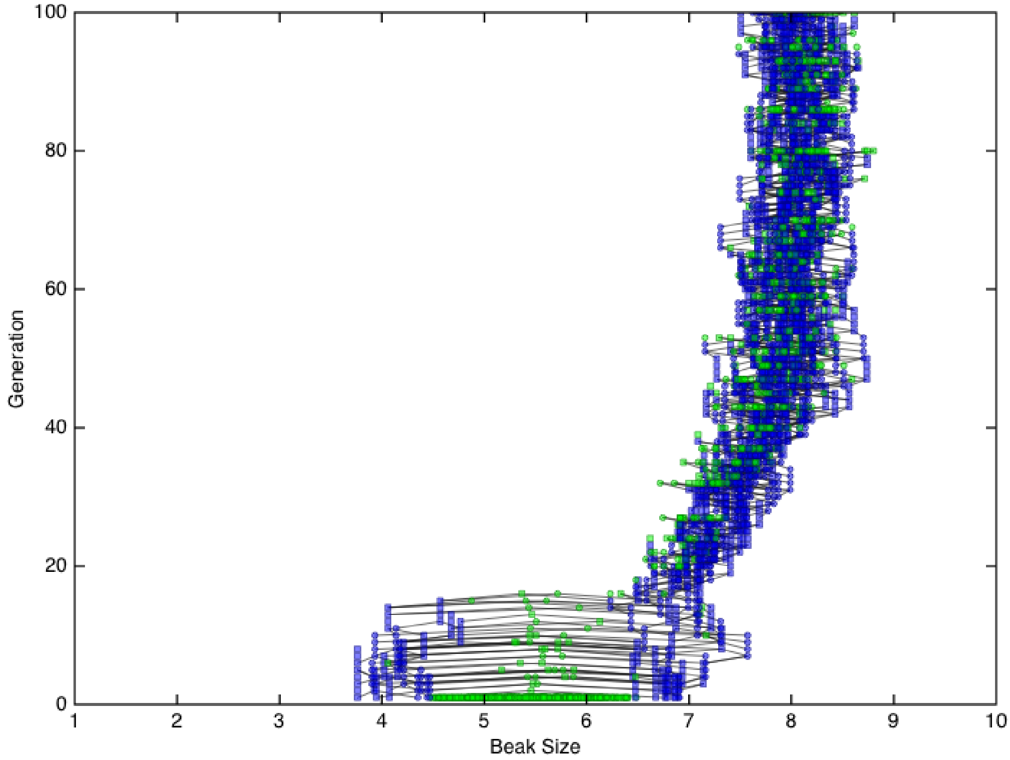

Figure 6.24: BSRM, Generation 1–100, Run 7. A representative example of left branch extinction after generation 10 and before generation 100.

Interestingly, in Run 23, shown in Figure 6.27, the right branch appears to contain a thin, thread like-branch which dramatically increases in width after generation ten.

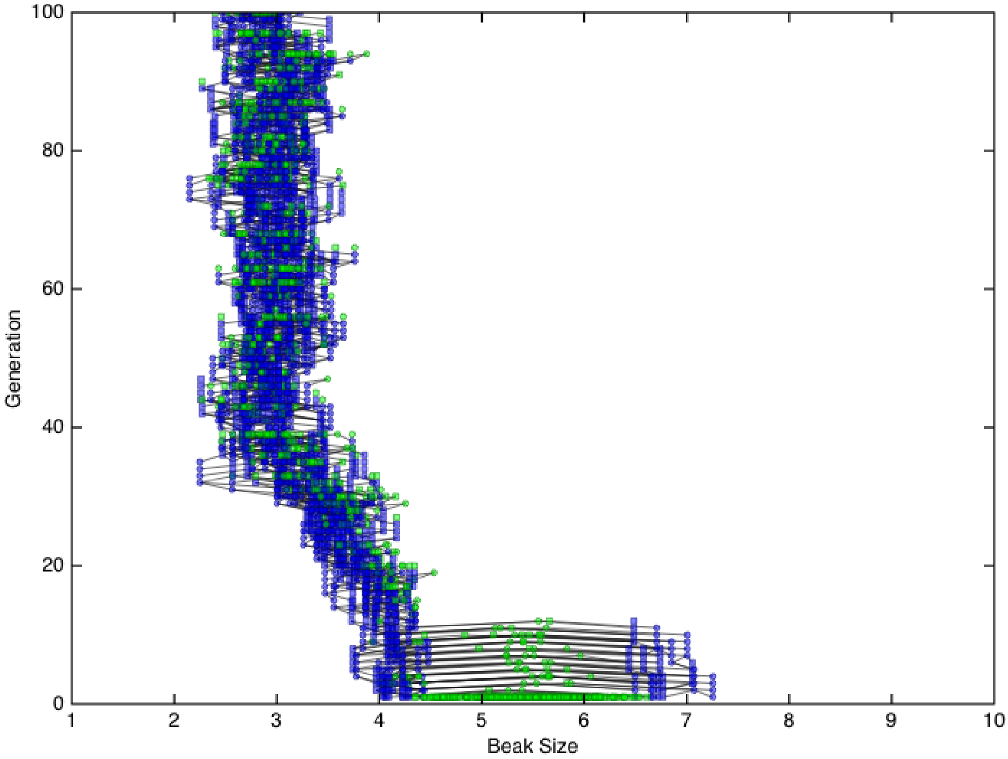

Figure 6.25: BSRM, Generation 1–100, Run 18. A representative example of right branch extinction after generation 10 and before generation 100.

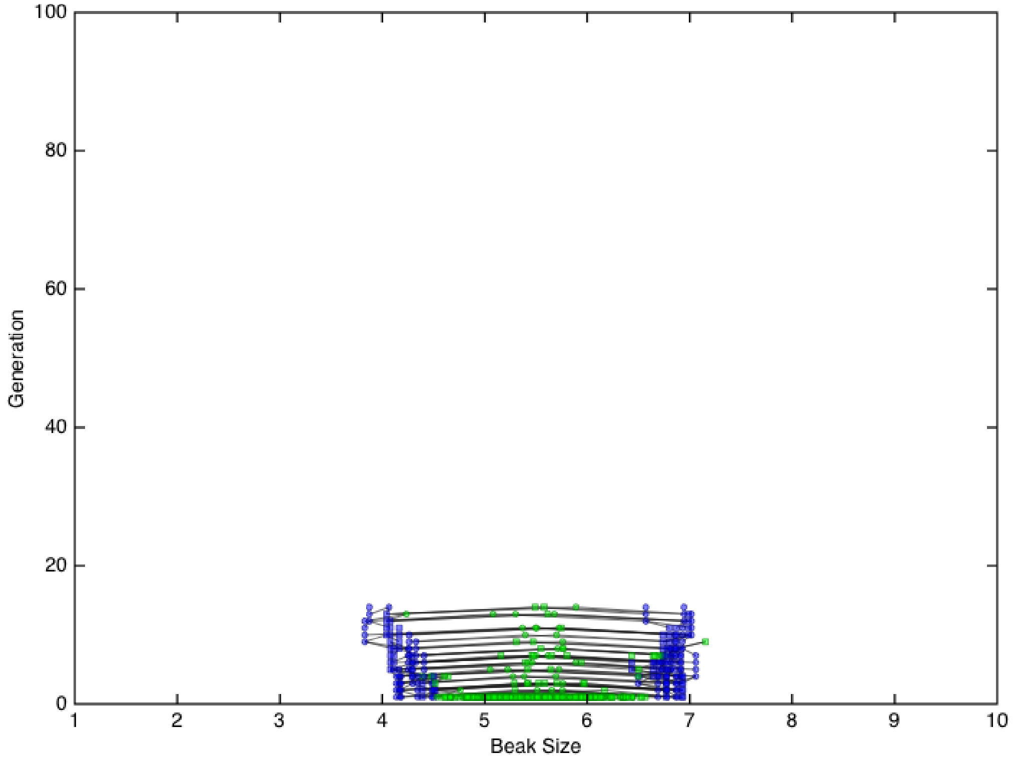

Figure 6.26: BSRM, Generation 1–100, Run 26. A representative example of complete extinction after generation 10 and before generation 100.

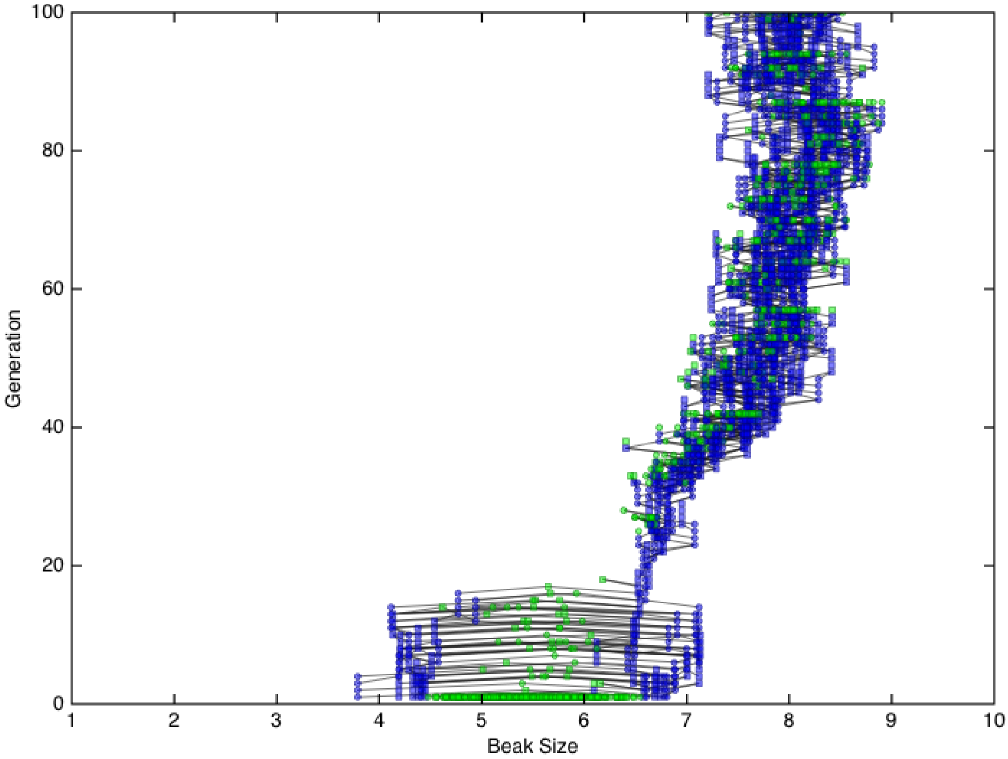

Figure 6.27: BSRM, Generation 1–100, Run 23. The single example of a thin, thread-like branch.

Generation 1–1000 Plots

The first 1000 generations for BSRM Run 1 are shown in Figure 6.28 as a prototypical example. The defining feature for BSRM is the convergence to a single population with an average beak size of three or eight. The results look very similar to the BSAM case except that only one population is supported. A single population with an average beak size of three is clearly stable up to generation 1000. As is the case for BSAM the high amount of variability in the individuals is clearly visible.

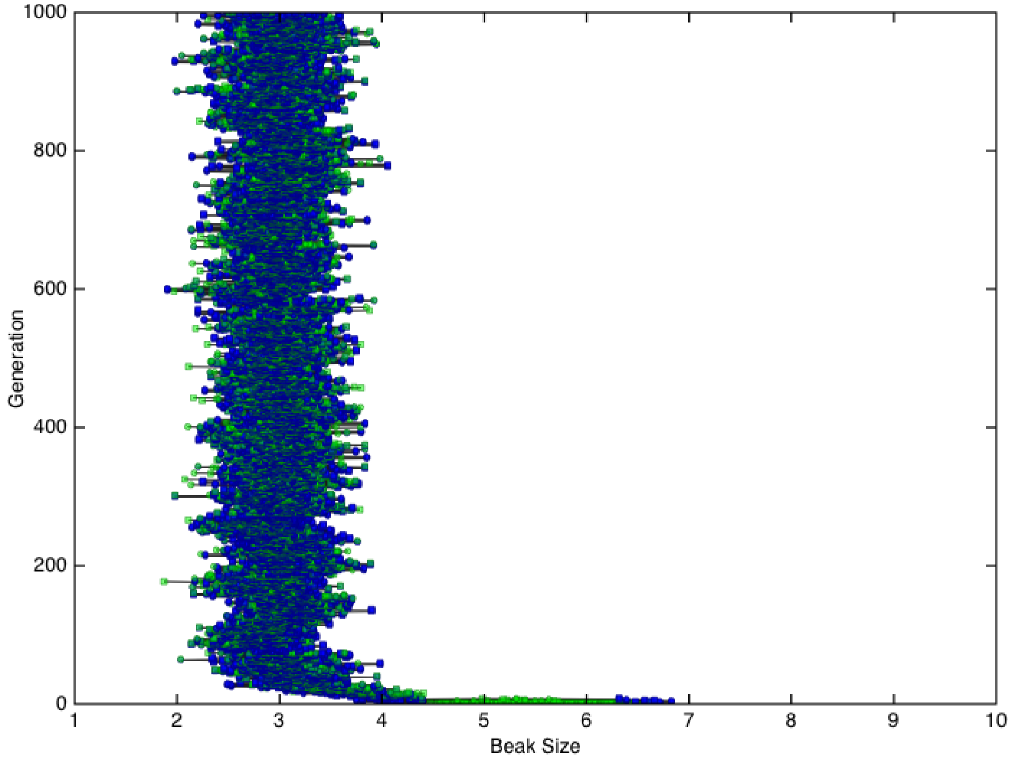

Figure 6.28: BSRM, Generation 1–1000, Run 1. A representative example of a single population, centered on one of the two distinct seed sizes, present in the last generation.

Complete extinction after generation 100 and before generation 1000 is a rare event. In one repetition, Run 12 (Figure 6.29), the right branch went extinct around generation 250. In two repetitions, the left branch went extinct. In Run 25 the left branch went extinct around generation 950, and in Run 35 the left branch went extinct around generation 600.

See Figure 6.30 for a representative example. Complete extinction did not occur in this interval.

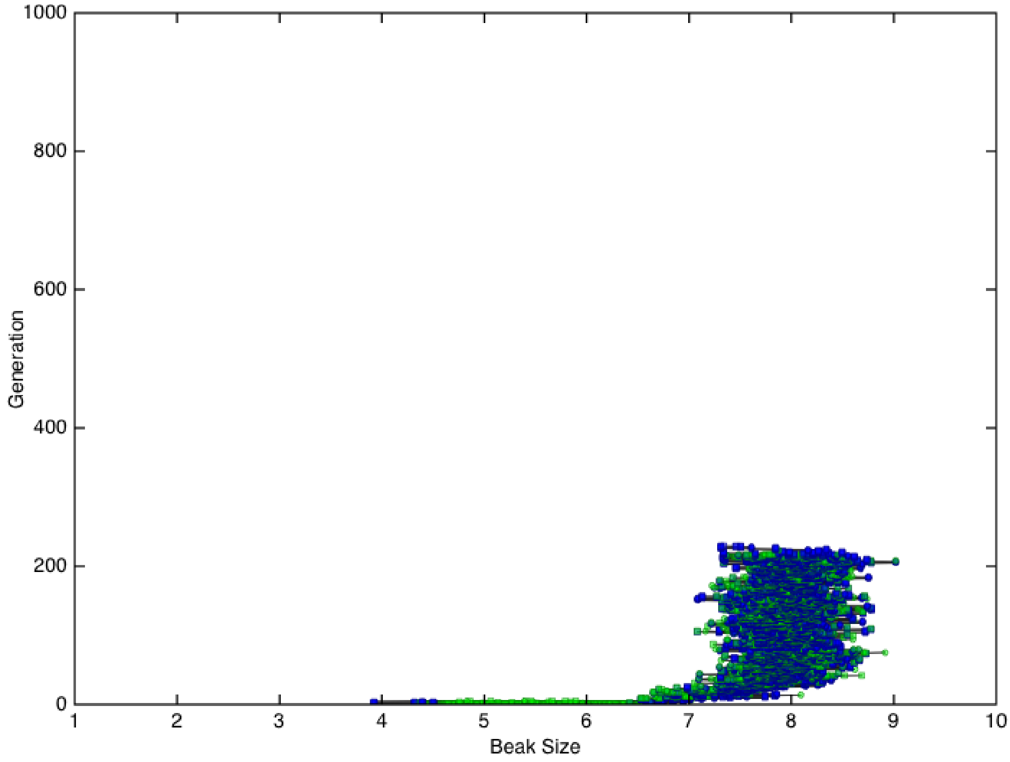

Figure 6.29: BSRM, Generation 1–1000, Run 12. A representative example of right branch complete extinction after generation 100 and before generation 1000.

In 41 of the repetitions a single population, centered on one of the two distinct seed sizes, was present in the last generation. See Run 1 (Figure 6.28) for a representative example. In the remaining seven repetitions, there were zero populations in the final generation. See Run 6 (Figure 6.31) for a representative example.

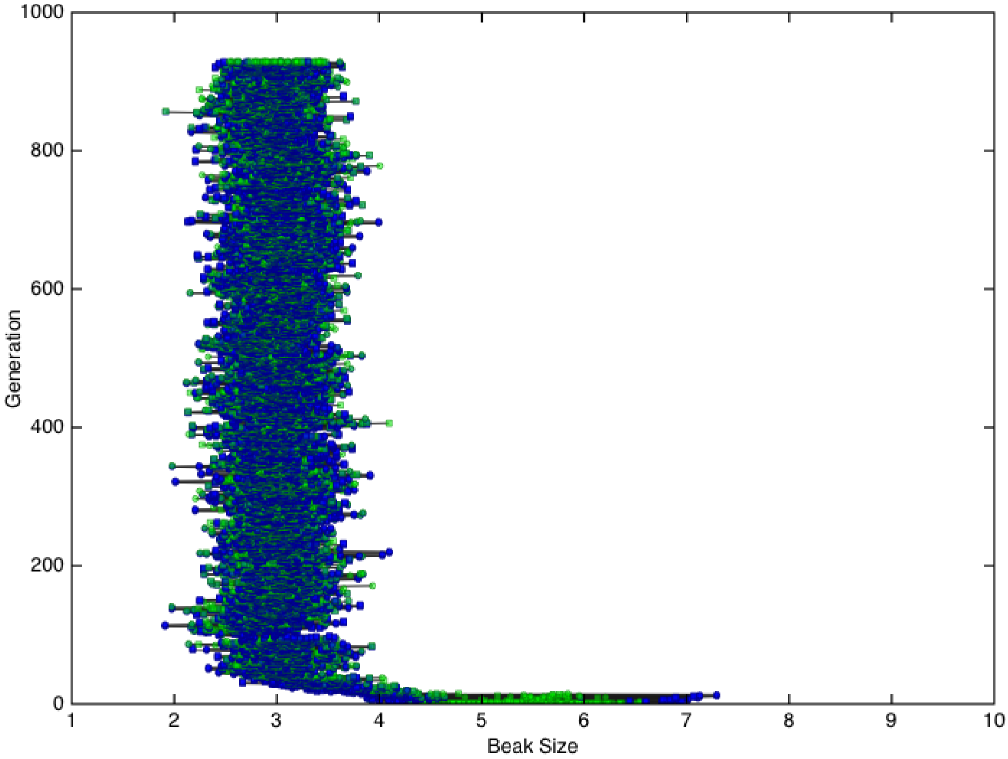

Figure 6.30: BSRM, Generation 1–1000, Run 25. A representative example of left branch complete extinction after generation 100 and before generation 1000.

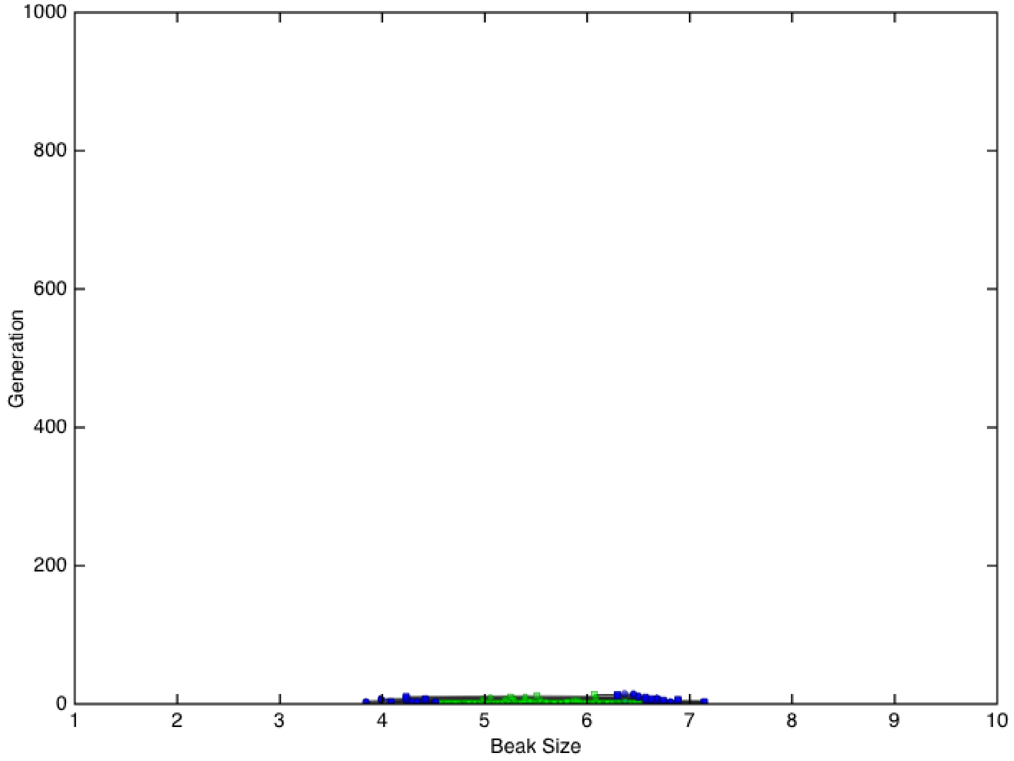

Figure 6.31: BSRM, Generation 1–1000, Run 6. A representative example of zero populations in the last generation.

6.2.3 Uniform Seeds & Assortative Mating

The results for USAM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for USAM Run 1 are shown in Figure 6.32 as a prototypical example. Like BSAM, a large portion of the initial population (first generation, after natural selection) dies leaving only the individuals near the tails. The main difference here is the seed distribution. In BSAM, the seed distribution is bimodal meaning there are two distinct seed sizes with few seeds of intermediate size—the initial population distribution clearly did not match the available seed distribution. In USAM, the mismatch is more subtle. The seed distribution is uniform so there are seeds available for birds with medium beak sizes, however, there are not enough to support a large density of individuals for 100 days.

In four repetitions (Run 10, 24, 29, and 36) only the left branch went extinct. See Figure 6.33 for a representative example. In nine repetitions (Run 1, 2, 13, 16, 32, 42, 43, 44, and 48) only the right branch went extinct. See Figure 6.34 for a representative example. In 13 repetitions (Run 5, 6, 7, 8, 22, 26, 31, 38, 39, 40, 45, 46, and 47) both branches went extinct. See Figure 6.35 for a representative example. In the 22 remaining repetitions both of the branches remain stable up to generation 10. See Figure 6.36 for a representative example.

A bias in the initial sex ratio can lead to rapid branch extinction. In 18 repetitions (Run 1, 5, 6, 7, 8, 10, 13, 26, 29, 31, 38, 39, 40, 42, 43, 46, 47, 48) a branch went extinct due to the lack of females. See Figure 6.33 for a representative example. In 13 repetitions (Run 2, 6, 16, 22, 24, 26, 31, 32, 38, 39, 44, 46, 47) a branch went extinct due to the lack of males. See Figure 6.34 for a representative example. In one repetition, Run 45 (Figure 6.37) both branches went extinct due to the lack of males. Interestingly, in two repetitions (Run 36, 40) there were no individuals in the left branch after natural selection. See Figure 6.38 for a representative example.

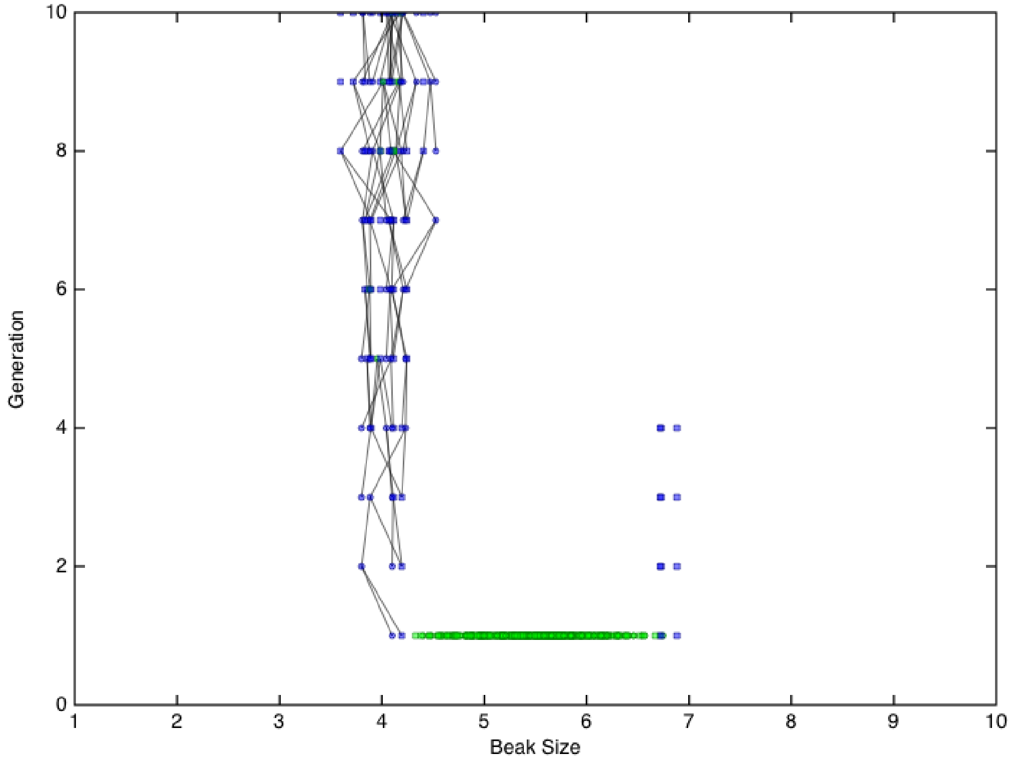

Figure 6.32: USAM, Generation 1–10, Run 1. A prototypical example of a population supporting a single branch.

All of the extinctions in the previous paragraph were due to rapid extinction. In two repetitions (Run 26, 31) a branch went extinct due to gradual extinction. See Figure 6.39 for a representative example.

In Run 3 (Figure 6.36), the variability in the right branch has increased to the point where it appears to be splitting into two new populations. In Run 5 (Figure 6.35), both of the left and right branches contain only males which leads to rapid extinction. In Run 22 (Figure 6.40), both the initial populations contain only females which leads to rapid extinction. In Run 6 (Figure 6.42) the left branch contains a single male and the right branch contains only females which also leads to rapid extinction. Interestingly, in Run 24 (Figure 6.41), the initial left population contains a single individual, a female, who lives for four years and produces no offspring.

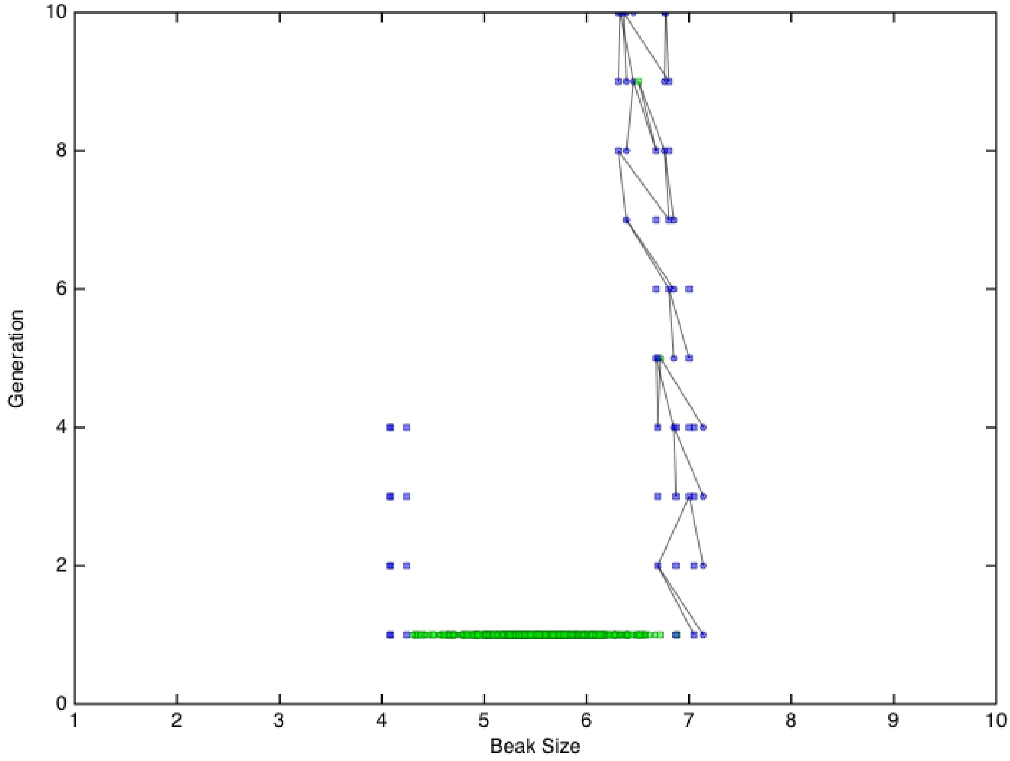

Figure 6.33: USAM, Generation 1–10, Run 10. A representative example of left branch rapid extinction due to a lack of females.

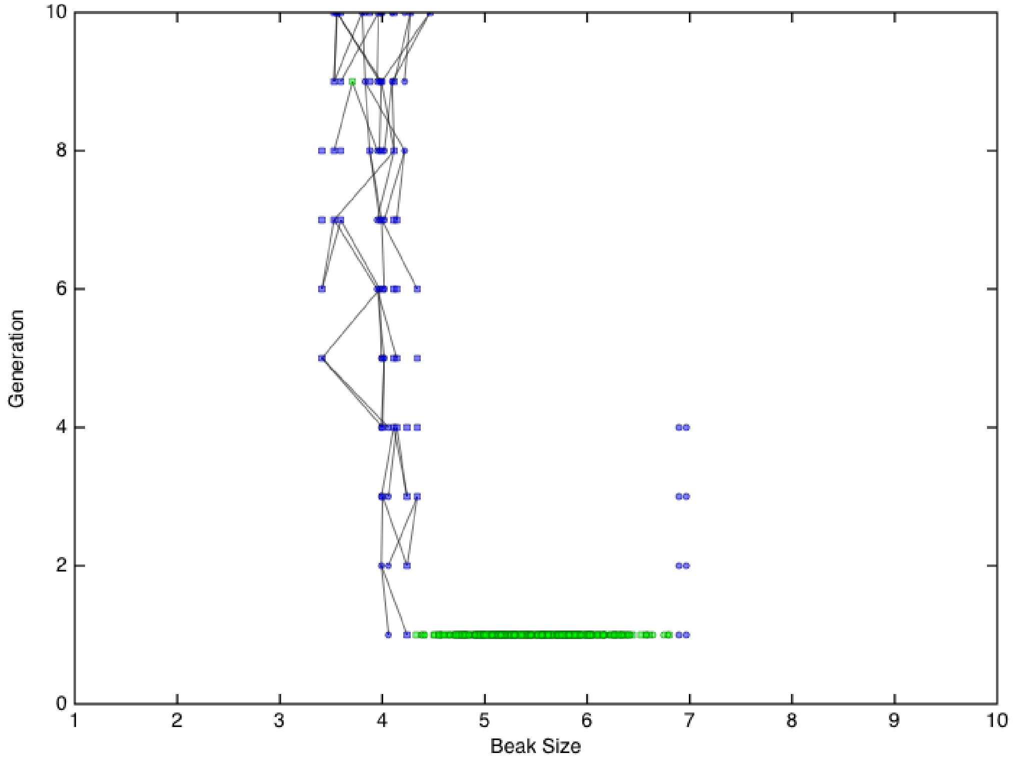

Figure 6.34: USAM, Generation 1–10, Run 2. A representative example of right branch rapid extinction due to a lack of males.

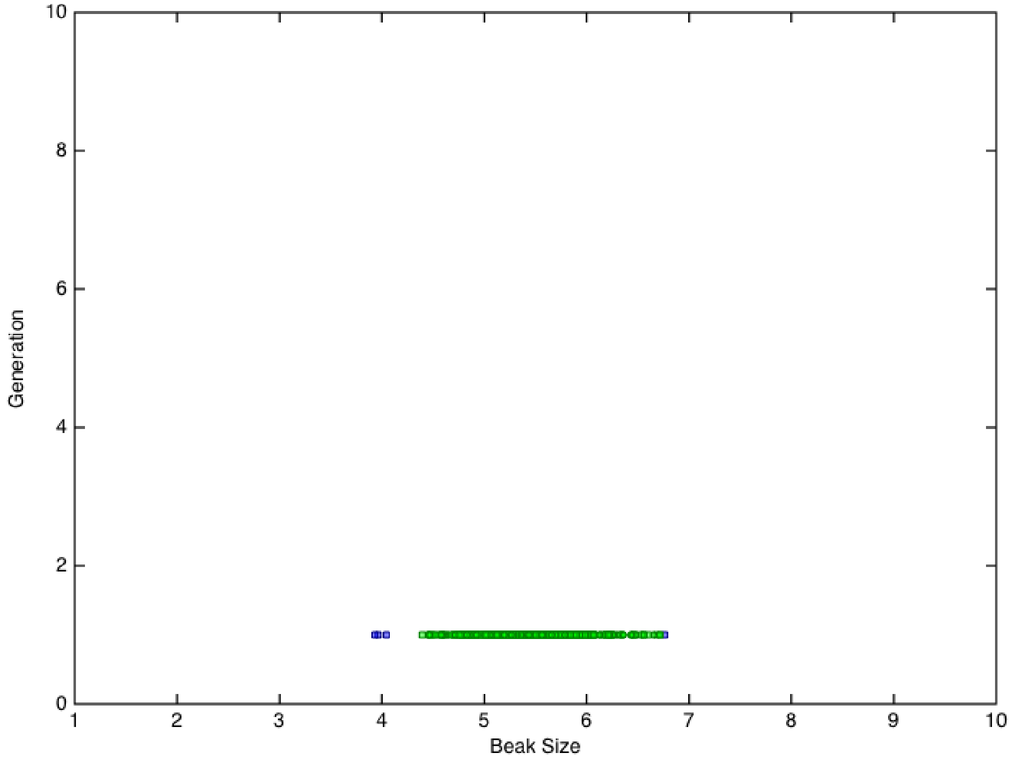

Figure 6.35: USAM, Generation 1–10, Run 5. A representative example of a population where the left and right branches contain only males which leads to rapid extinction.

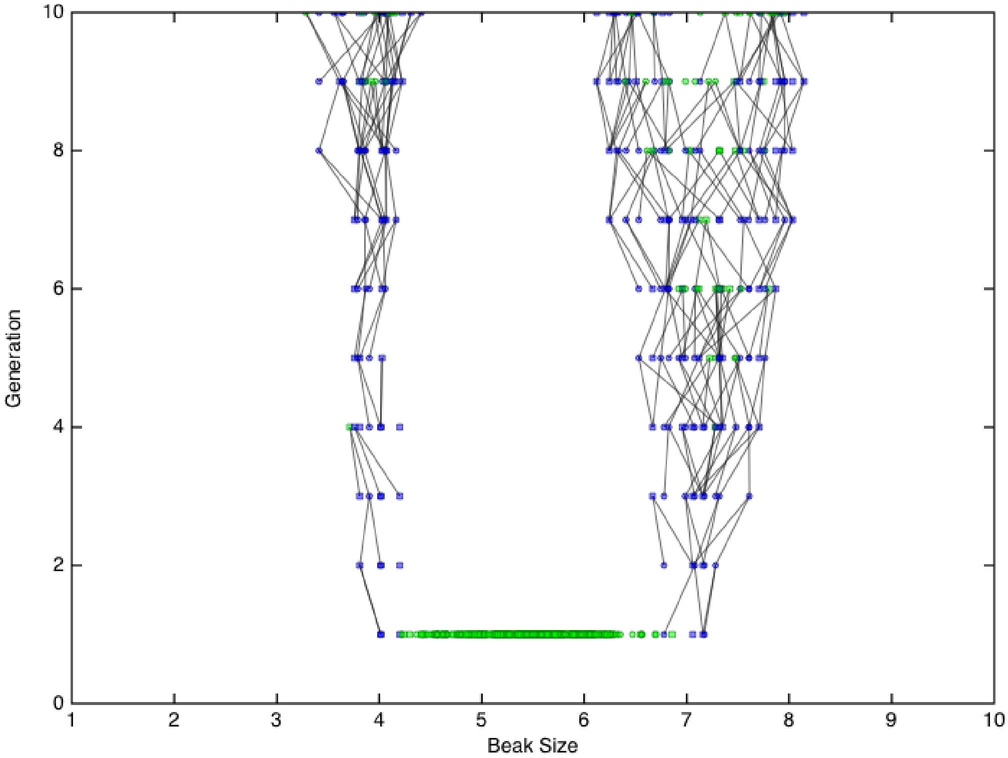

Figure 6.36: USAM, Generation 1–10, Run 3. A representative example of a population where both branches remain stable up to generation 10, and the variability in the right branch increases to the point where it appears to be splitting into two new populations.

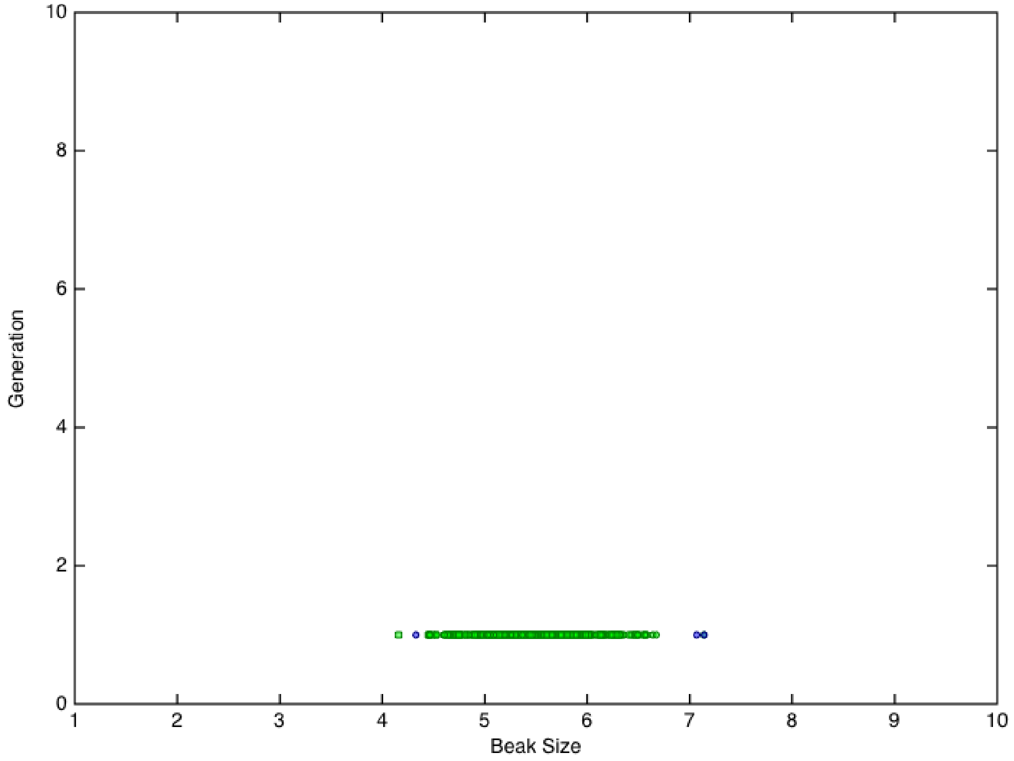

Figure 6.37: USAM, Generation 1–10, Run 45. The single example of a population where both branches go extinct due to the lack of males.

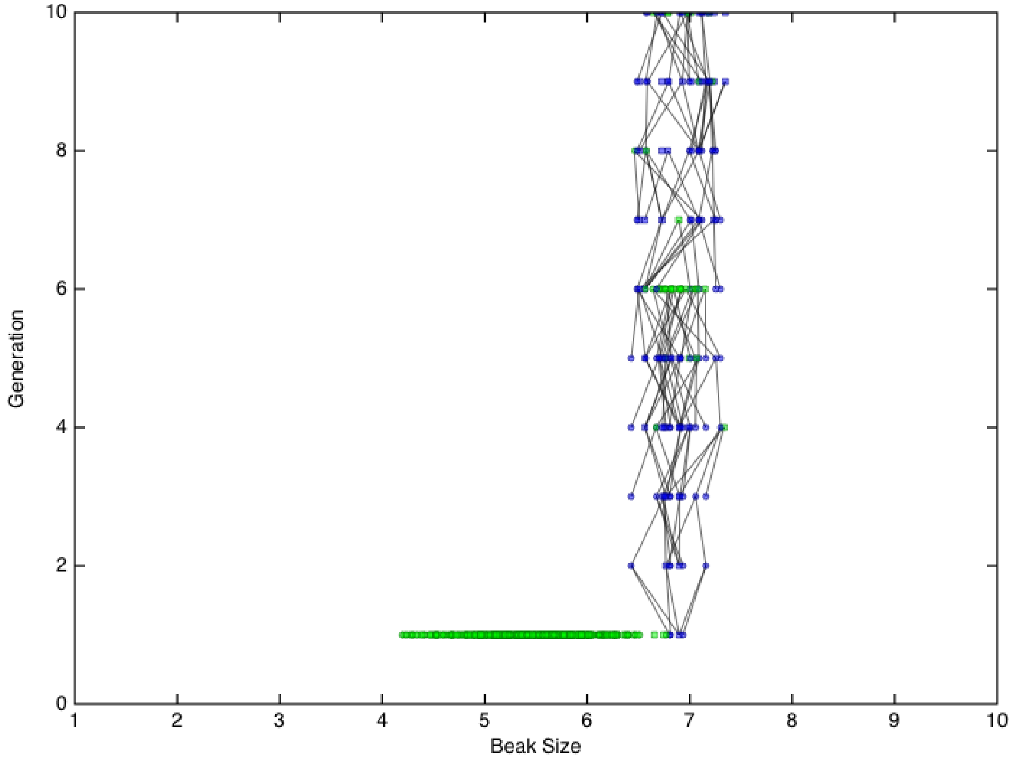

Figure 6.38: USAM, Generation 1–10, Run 36. A representative example of a population where there are no individuals in the left branch (after natural selection).

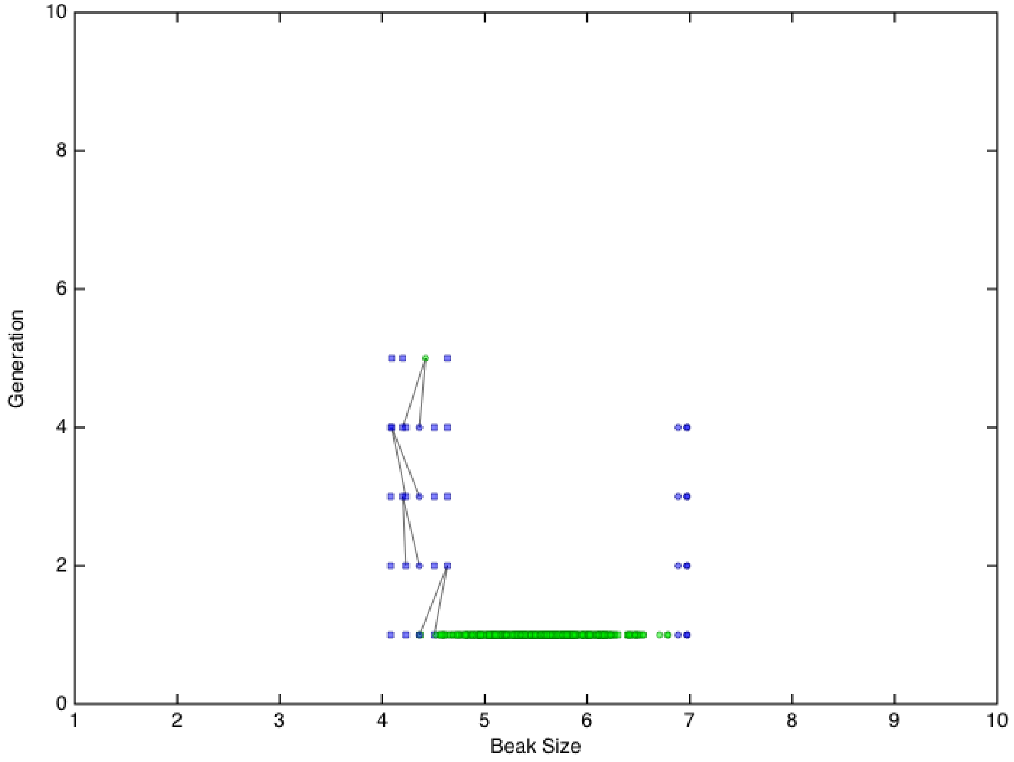

Figure 6.39: USAM, Generation 1–10, Run 26. A representative example of gradual (left) branch extinction.

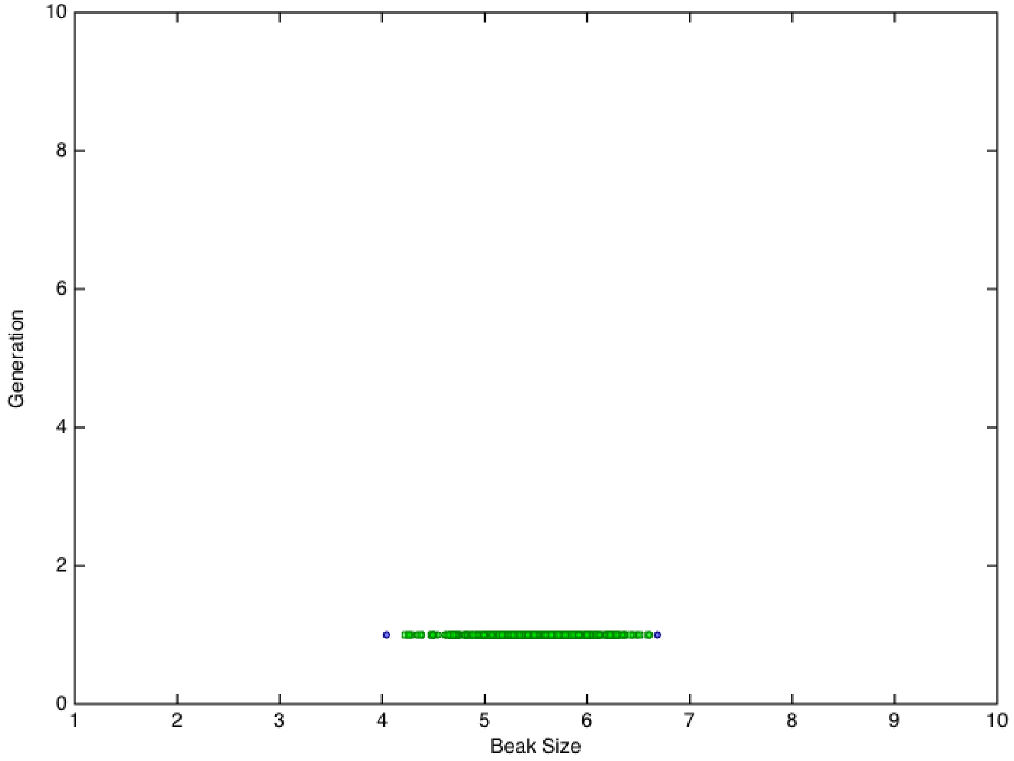

Figure 6.40: USAM, Generation 1–10, Run 22. A representative example where both branches only contain females which leads to rapid extinction.

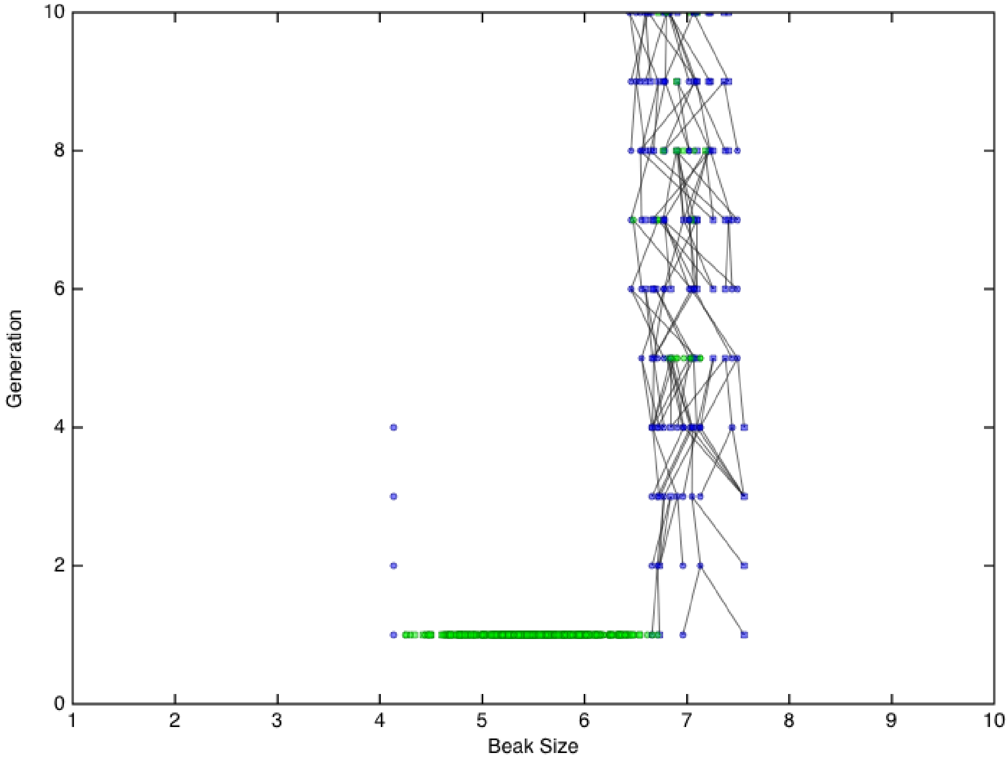

Figure 6.41: USAM, Generation 1–10, Run 24. A representative example where the left branch contains a single female, who lives for four years and produces no offspring.

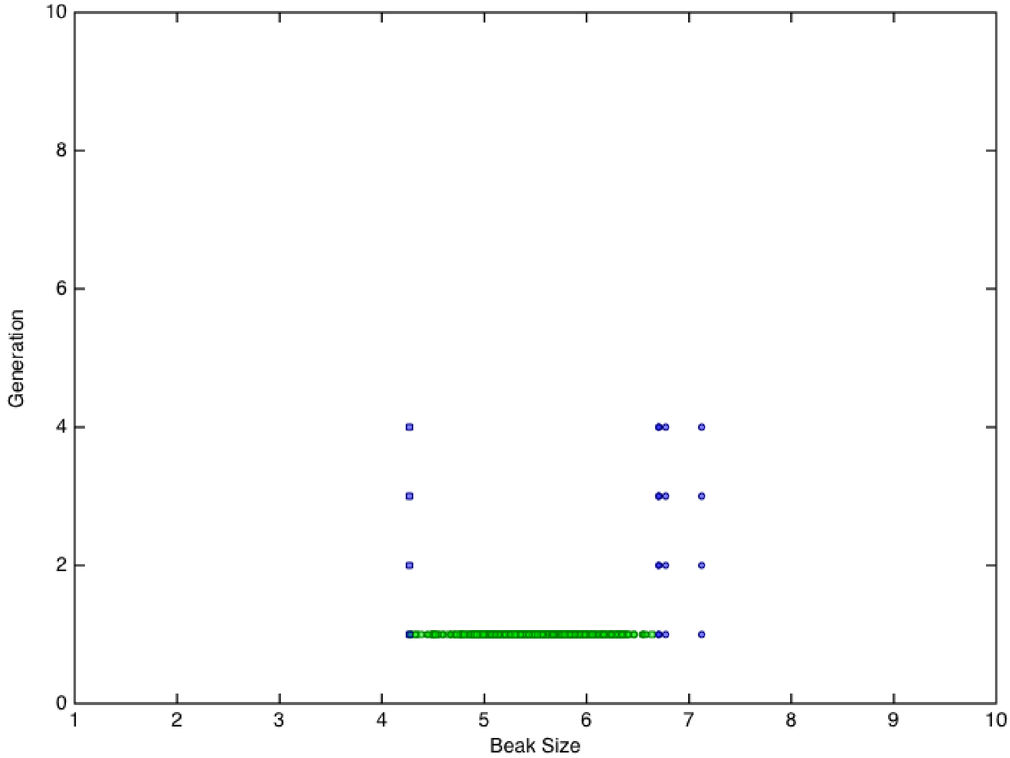

Figure 6.42: USAM, Generation 1–10, Run 6. A representative example where the left branch contains a single male, and the right branch contains only females which leads to rapid extinction.

Generation 1–100 Plots

The first 100 generations for USAM Run 1 are shown in Figure 6.43 as a prototypical example. The defining characteristic for USAM is the branching and merging. As with the three other cases, there was a large-scale reduction in the initial population (first generation, after natural selection). As with BSAM, two smaller populations emerged from the tails of the original population. Unlike the BSAM case, the initial populations went on to produce additional branches. It also appears that isolated populations remain at least one beak unit apart with respect to the edges of their populations.

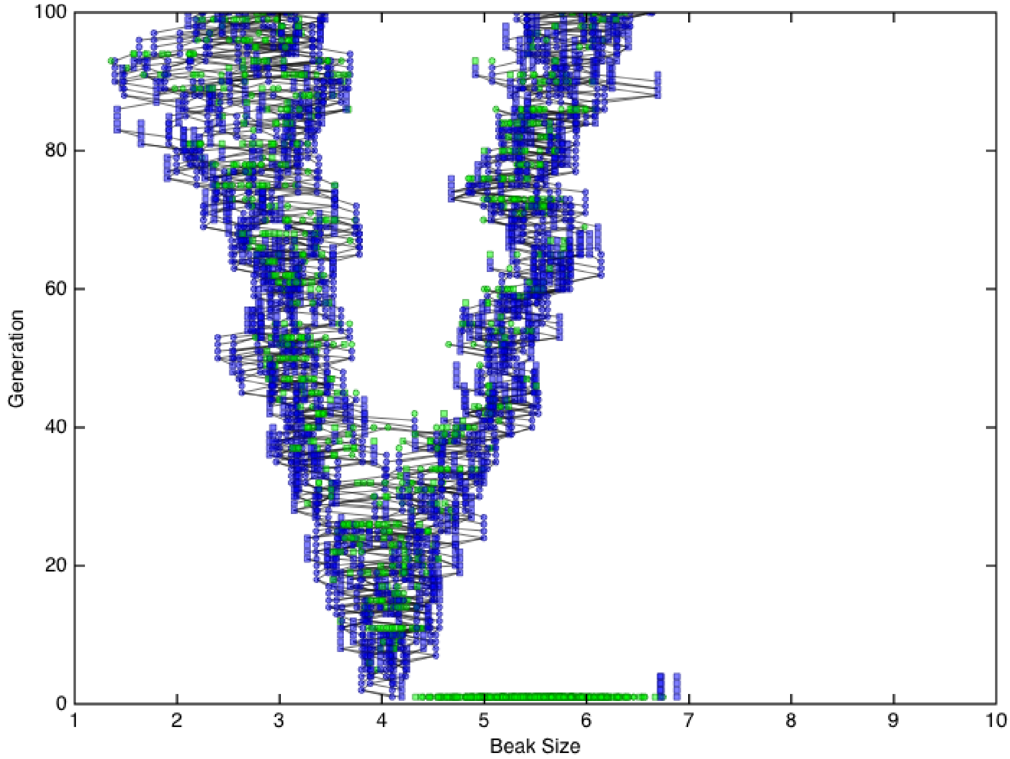

Figure 6.43: USAM, Generation 1–100, Run 1. A prototypical example of a branching population.

For example, the left branch splits and forms two new populations. It appears that the initial divergence is due to repeated die-off of the population during natural selection as indicated by the green/light bars. The population density near the center of the left branch is gradually reduced and around generation 40 the branch cleanly splits into two new populations.

Extinction after generation 10 and before generation 100 is an unlikely event. In three repetitions (Run 15, 28, 34), the left branch went extinct around generation 65. See Figure 6.44 for a representative example. Extinction did not occur for the right branch during this interval.

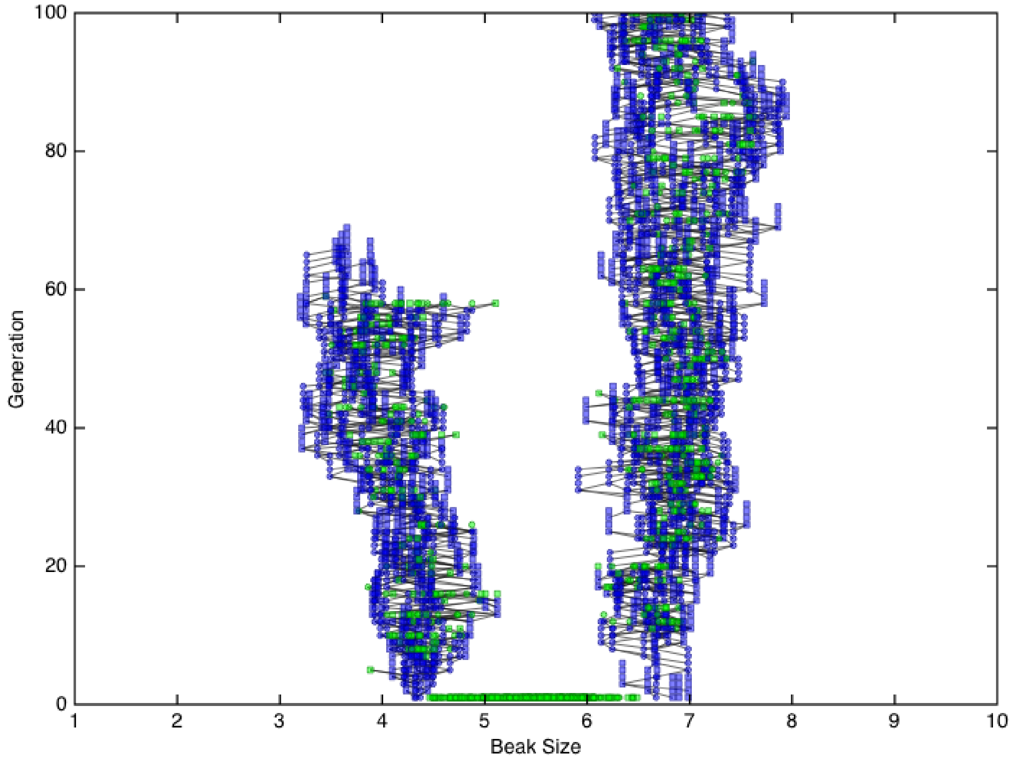

Figure 6.44: USAM, Generation 1–100, Run 15. A representative example where the left branch goes extinct after generation 10 and before generation 100.

In Run 3 (see Figure 6.45), an example of early branching is demonstrated. The right population undergoes rapid expansion, developing a large amount of variation by generation 10 and splits into two subpopulations. The two subpopulations briefly produce hybrid offspring around generation 20 and again later near generation 100.

In Run 10 (see Figure 6.46), the right branch splits into two new branches with lim-

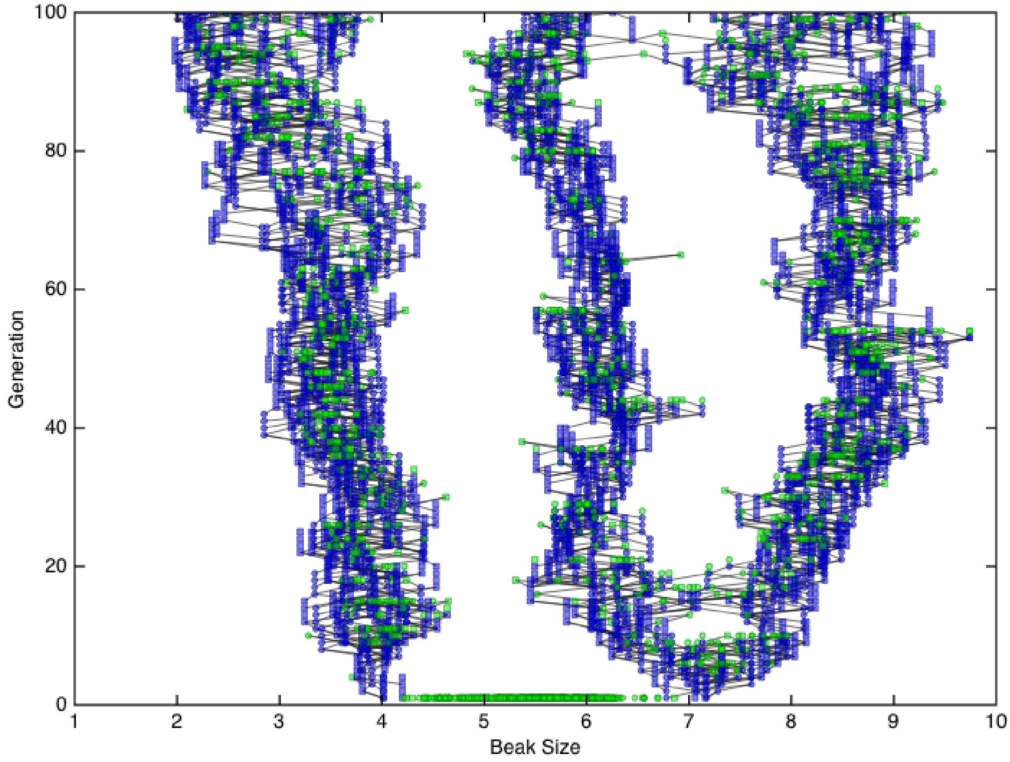

Figure 6.45: USAM, Generation 1–100, Run 3. A representative example of early (right) branching.

ited interbreeding until generation sixty when they become fully isolated. Then, around generation 90 they appear to be merging and splitting simultaneously.

In Run 24 (see Figure 6.47), there is an interesting helix-like structure in the right branch. Around generation 50 the population begins to branch, then merges at generation 65 only to split again at generation 75.

In Run 41 (see Figure 6.48), the right branch undergoes a split near generation 70. It appears that the two subpopulations are attempting to merge before generation 100. The right subpopulation shows a high amount of variability compared with the left subpopulation.

Run 44 (Figure 6.49) is an example of a loosely defined population. Around generation 80, the three populations appear to be much less distinct with considerable interbreeding taking place. Around generation 100, the population with the smallest beak size appears to

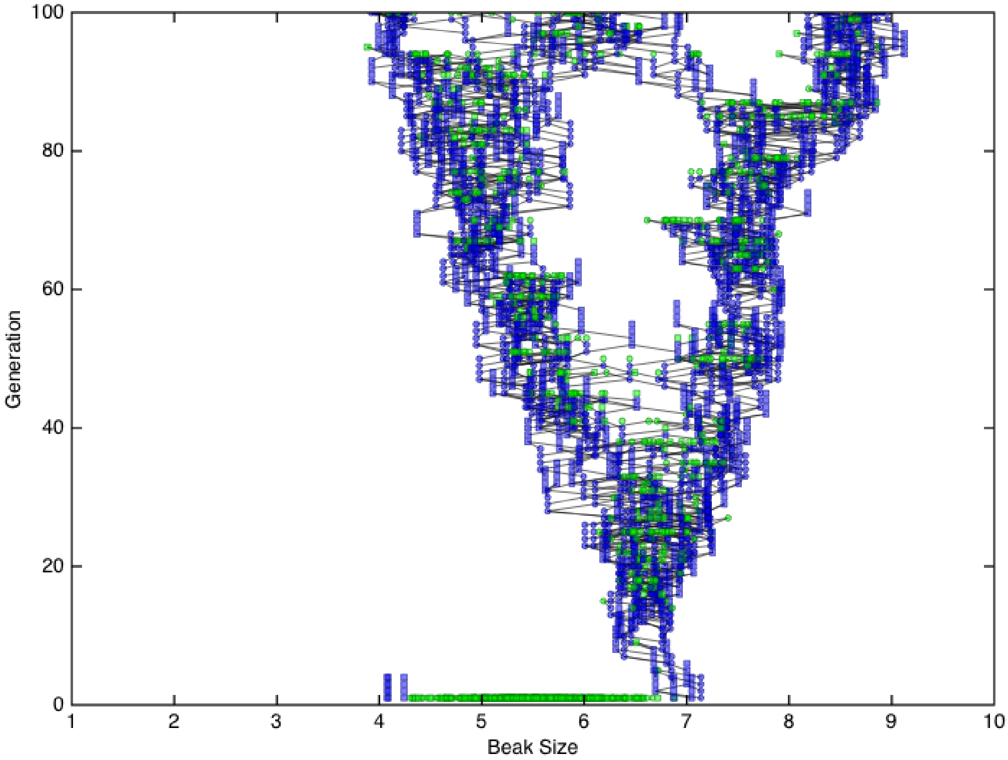

Figure 6.46: USAM, Generation 1–100, Run 10. A representative example of merging and splitting simultaneously (around generation 90).

be well defined while the other two populations remain somewhat disorganized.

The stability of new branches is not guaranteed. In Run 9, 12, 35, and 48, one of the new branches went extinct. In Run 12 and 48, the extinct population contained only males. See Figure 6.50 for a representative example. In Run 9 and 35, the extinct population contained only females. See Figure 6.51 for a representative example.

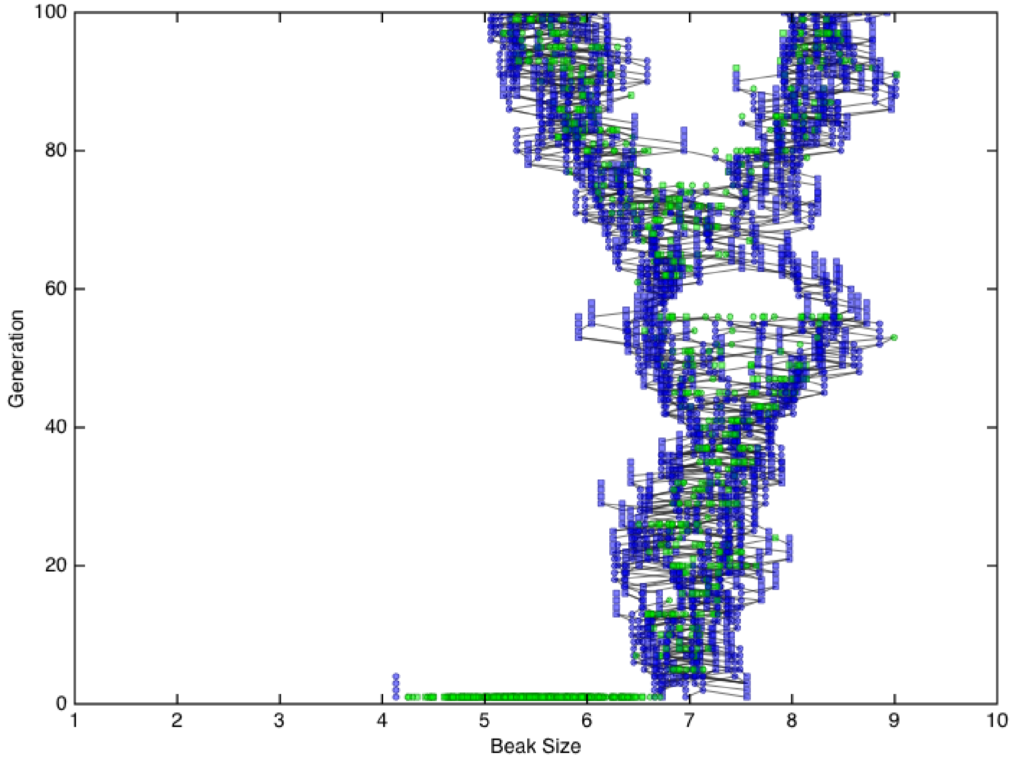

Figure 6.47: USAM, Generation 1–100, Run 24. A representative example of an interesting helix-like structure.

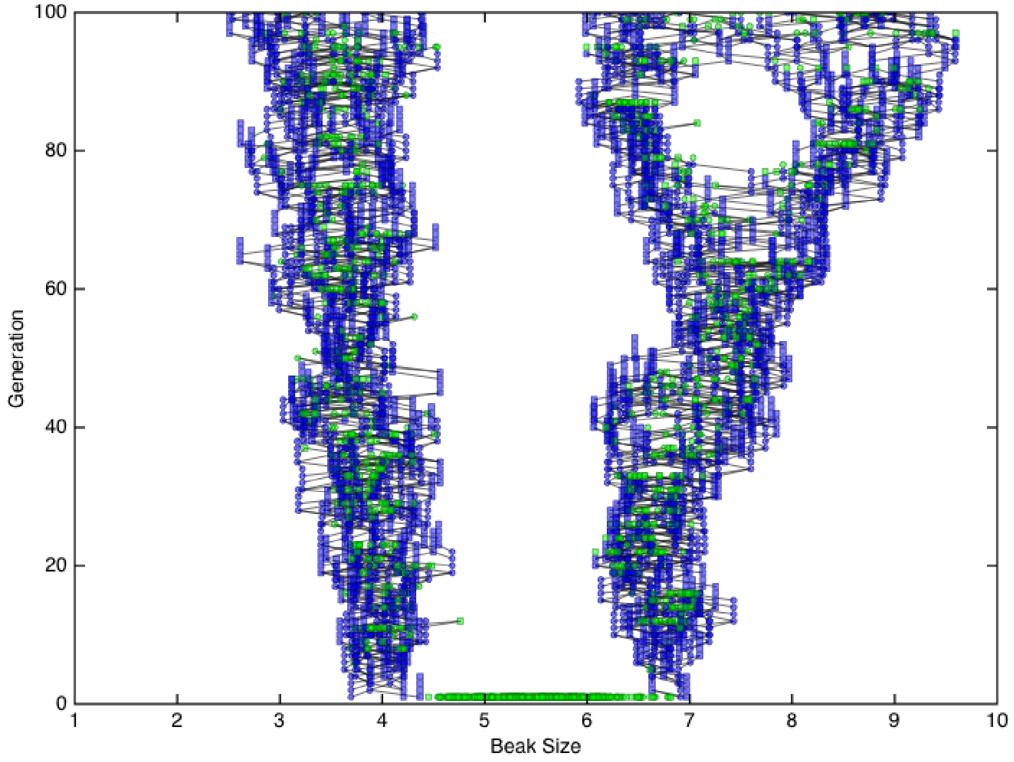

Figure 6.48: USAM, Generation 1–100, Run 41. A representative example of a branch with high variability.

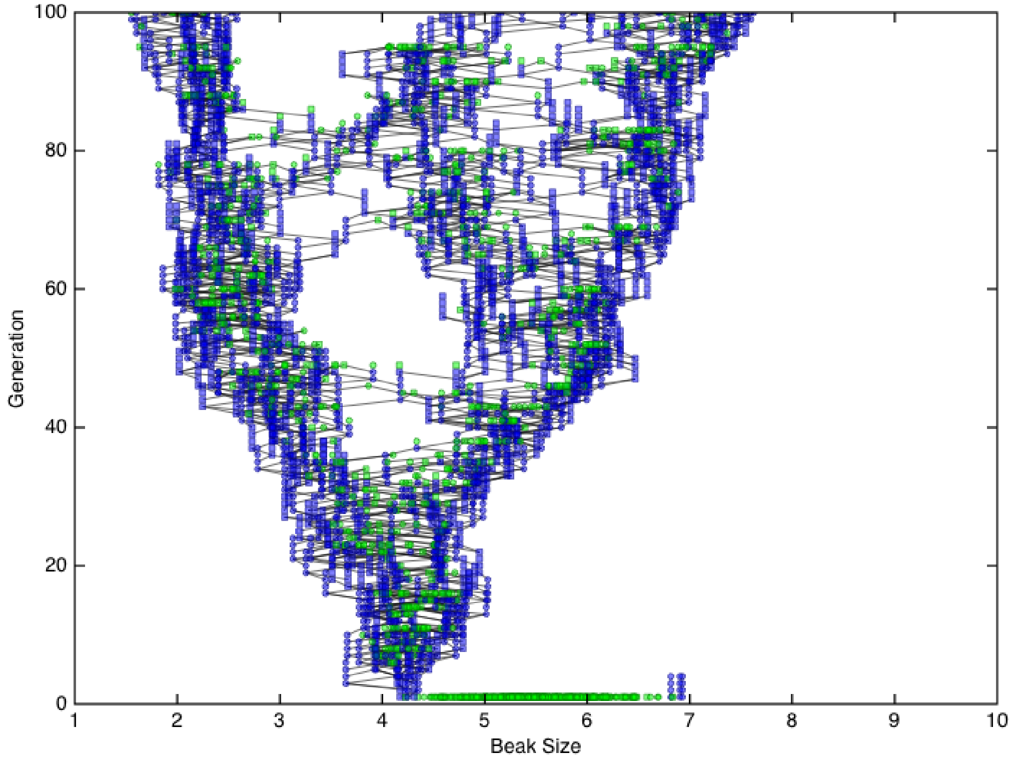

Figure 6.49: USAM, Generation 1–100, Run 44. A representative example of a loosely defined population.

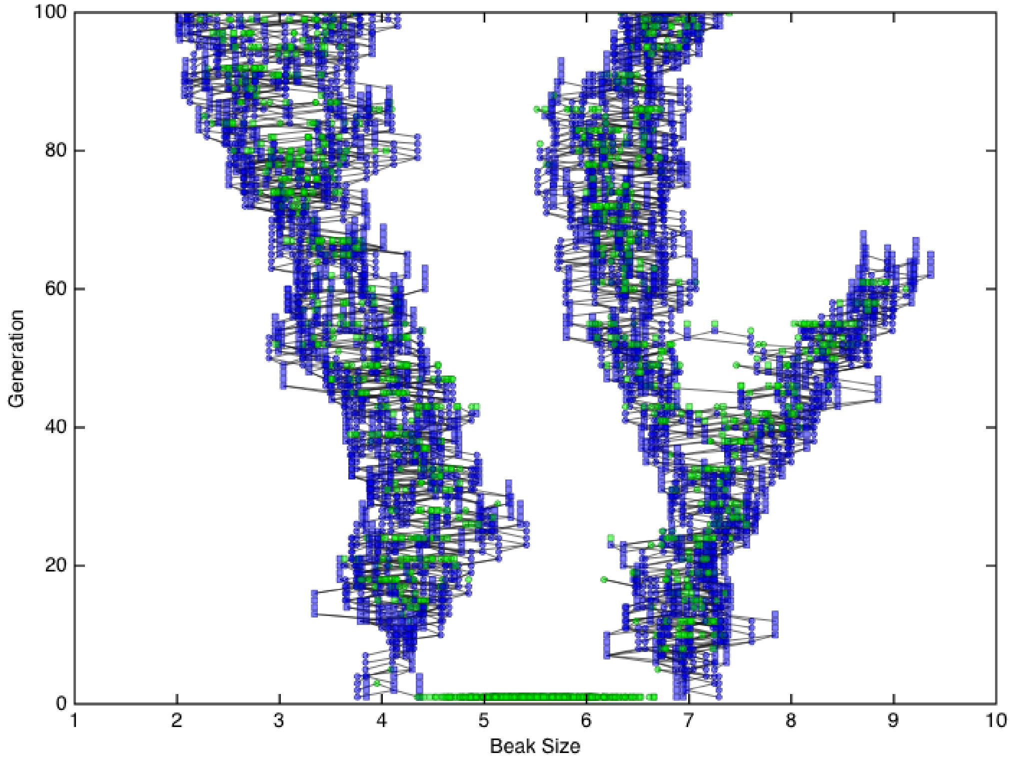

Figure 6.50: USAM, Generation 1–100, Run 12. A representative example of an extinct branch containing only males.

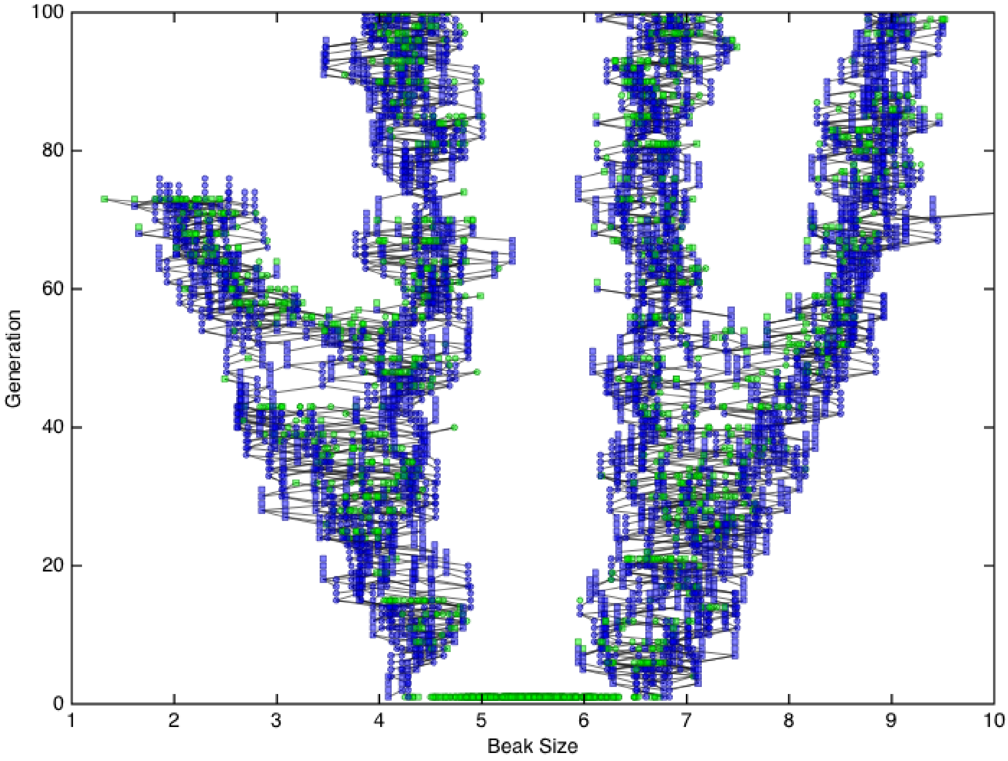

Figure 6.51: USAM, Generation 1–100, Run 35. A representative example of an extinct branch containing only females.

Generation 1–1000 Plots

The first 1000 generations for USAM Run 1 are shown in Figure 6.52 as a prototypical example. The defining characteristic for USAM is the repeated branching and merging—with more branching than merging. Here, populations are not fixed entities, when a population goes extinct another population moves into to fill the niche. Boundary effects appear to be present in that populations do not occupy the upper and lower limits of the food supply.

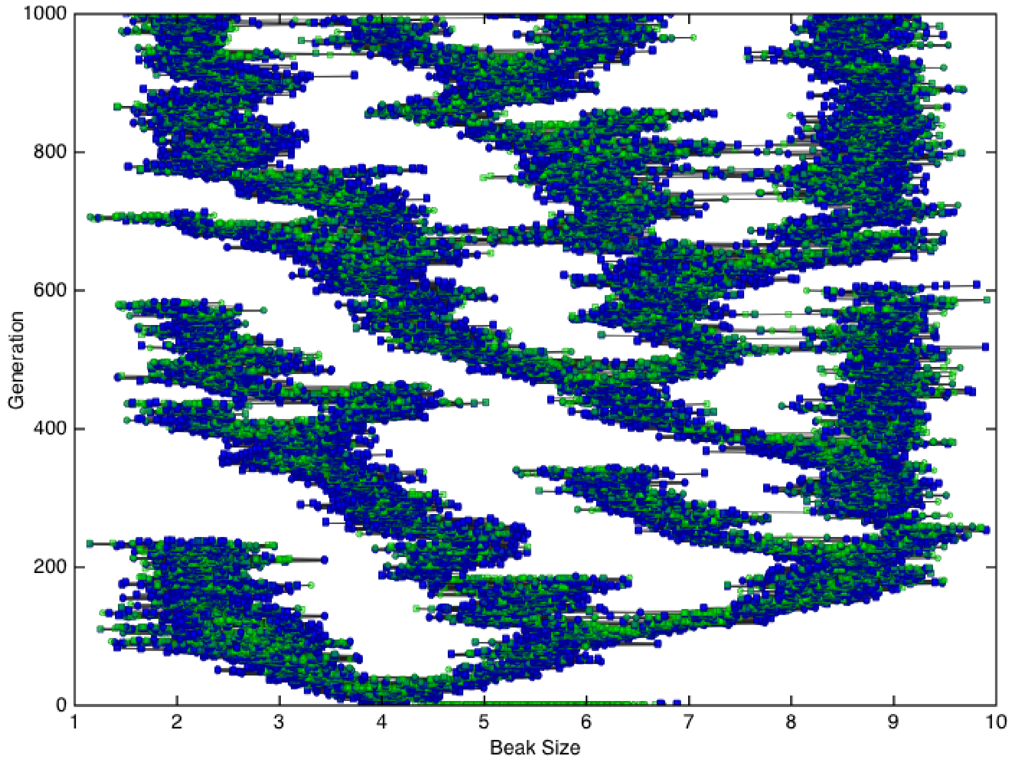

Figure 6.52: USAM, Generation 1–1000, Run 1. A representative example of repeated branching and merging along with the extinction of apparently stable branches.

The same pattern is repeated throughout each repetition—significant die-off in the center of a given population followed divergence and/or possible extinction. For example, just after generation 400 the branch with an average beak size near three splits into two populations which then merge back together a few generations later. Stability of new branches is not guaranteed. For example, the branch with an average beak size near 2.25 goes extinct just after generation two hundred. This is probably due to a sex ratio imbalance, which is a result of small population sizes. Also, a genetic drift component is present which causes a random wobble in each subpopulation.

In Run 23 (see Figure 6.53), the left initial population splits before generation 100. Around generation 175 the population with an average beak size of 5.0 produces hybrid offspring with the right initial population, all of which appear to be inviable and then goes extinct.

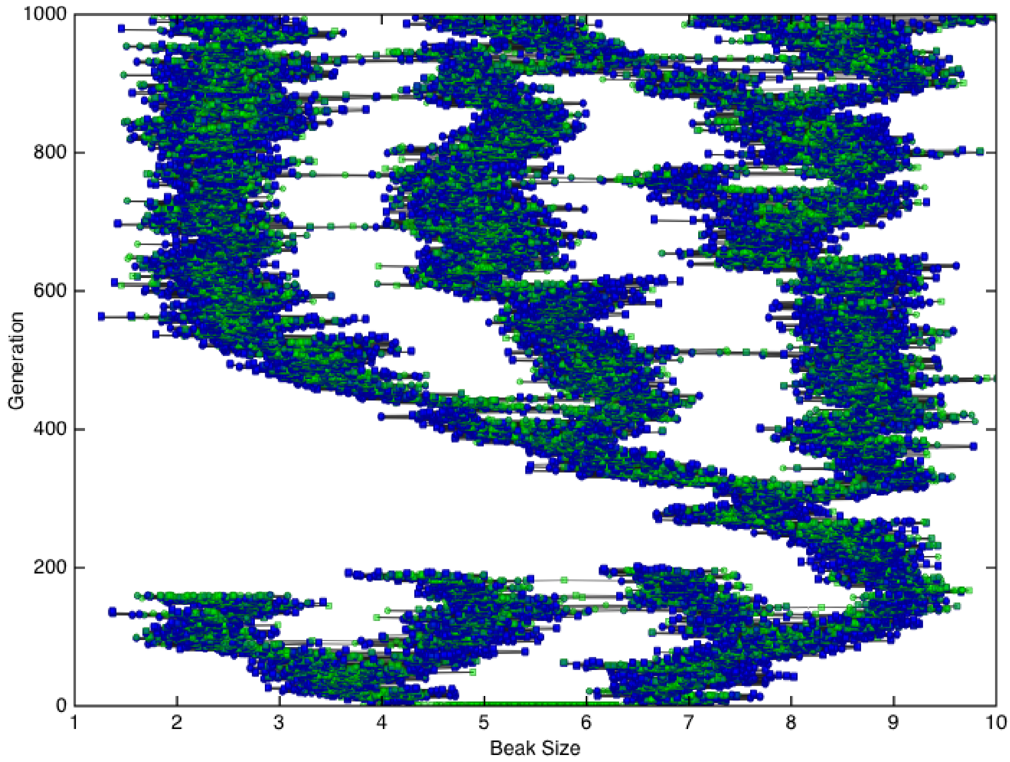

Figure 6.53: USAM, Generation 1–1000, Run 23. A representative example of repeated branching and merging along with the production of inviable hybrid offspring.

In the same run, the right initial population splits into two subpopulations. The left branch with an average beak size of seven goes extinct around generation 200 while the right branch shifts to the right (increasing beak size), stops before the boundary on the right and begins shifting to the left (smaller beak size) branching twice before encountering the left boundary.

There are typically multiple instances of apparently stable branches dying off in each repetition. For example, in Run 1 (Figure 6.52), the population with an approximate beak size of 2.2 around generation 200 dies off shortly after. In the same repetition, the population with an approximate beak size of 6.5 around generation 300 also goes extinct a few generations later.

We identified the number of populations in generation 1000. In a single repetition we found one population, in five repetitions we found two populations, in 19 repetitions we found three populations, and in 10 repetitions we found four populations. The remaining 13 repetitions ended in complete extinction.

6.2.4 Uniform Seeds & Random Mating

The results for USRM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for USRM Run 1 are shown in Figure 6.54 as a prototypical example. There is a initial large-scale die-off as seen in the USAM case. As with the BSRM case, offspring are produced with intermediate beak sizes. Unlike the BSRM case, a small but significant number of seeds are available which leads to rapid repopulation of the intermediate beak size range. For example, in Run 1, a green/light horizontal bar is present in the eighth generation, indicating a sizable die-off of the population similar to the first generation. After this die-off, the population quickly repopulates the niche.

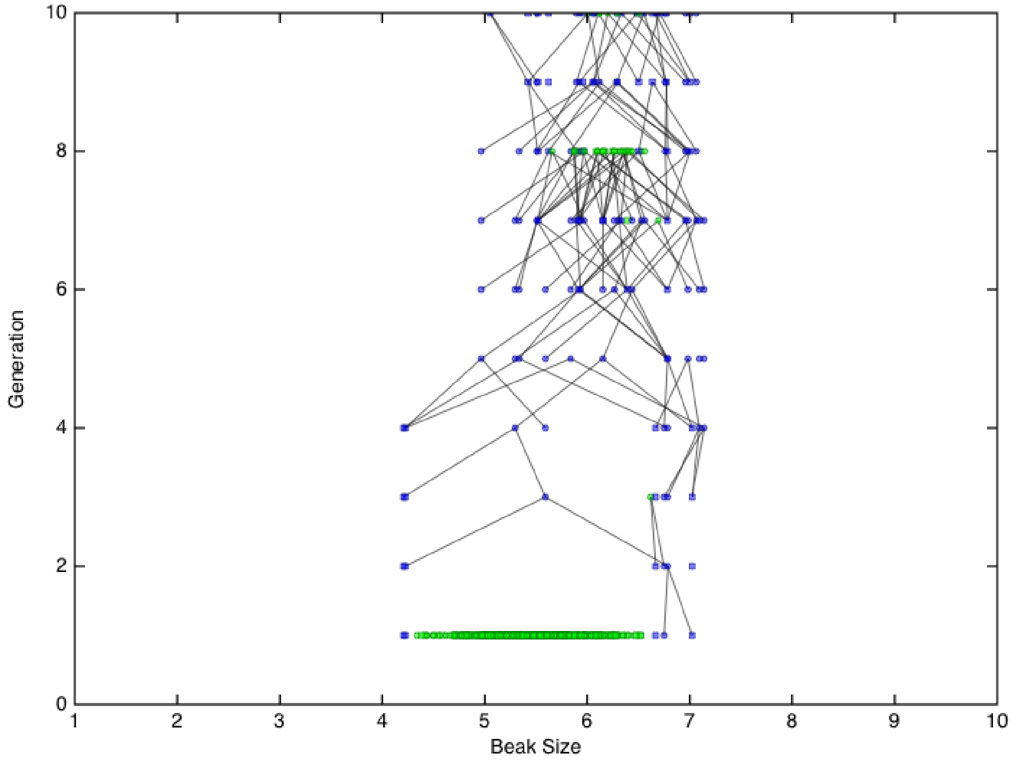

Figure 6.54: USRM, Generation 1–10, Run 1. A representative example of single population repopulating a niche after a sizable die-off.

In six repetitions (Run 6, 12, 24, 29, 31, 45) there was complete extinction. See Figure 6.55 for a representative example. In almost all of these cases (with Run 6 the exception) the population faced rapid extinction in which no reproduction took place.

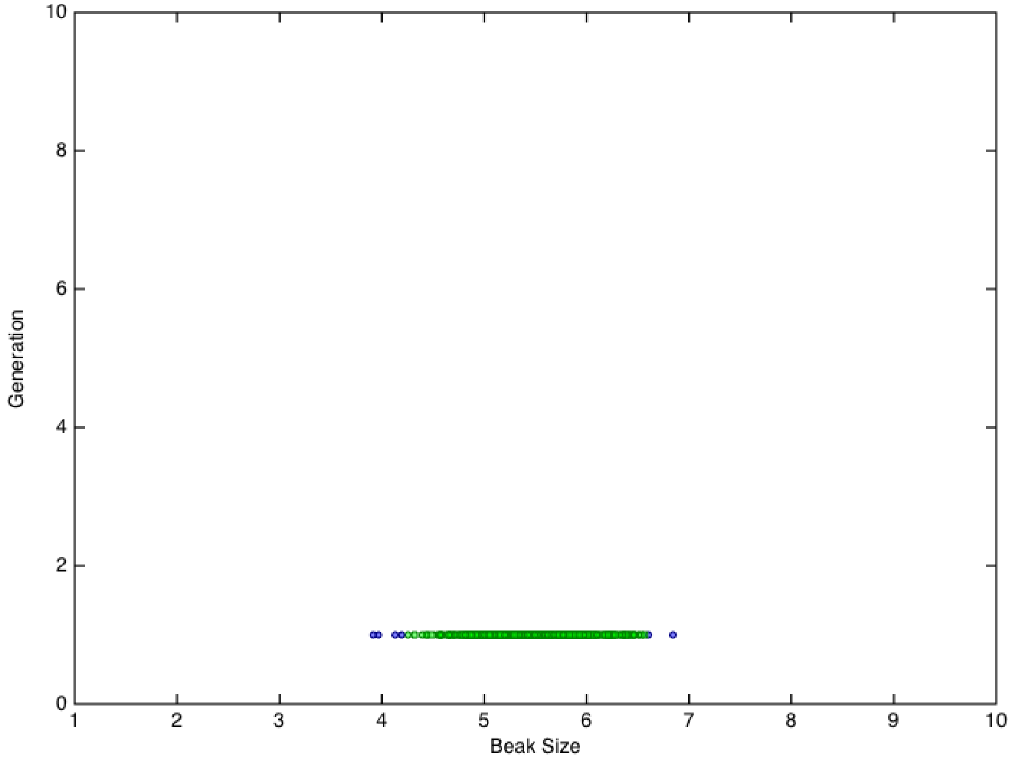

Figure 6.55: USRM, Generation 1–10, Run 12. A prototypical example of complete extinction due to the lack of males

In Run 6 (see Figure 6.56), the population went extinct after producing a limited number of viable offspring. The sparse graph is a result of an insufficient number of females produced in the population. This causes an imbalance in the sex ratio and eventually leads to extinction.

In three repetitions (Run 6, 31, 45) there was complete extinction due to the lack of females in the population. See Figure 6.56 for a representative example. In three repetitions (Run 12, 24, 29) there was complete extinction due to the lack of males in the population. See Figure 6.55 for a representative example.

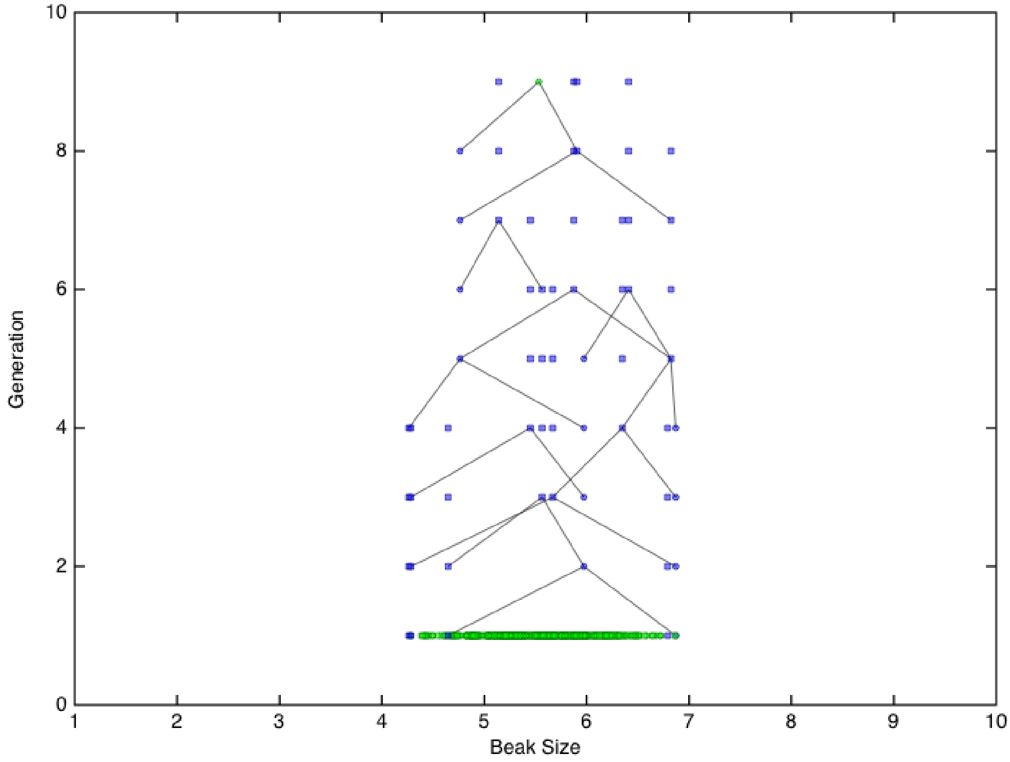

Figure 6.56: USRM, Generation 1–10, Run 6. A representative example of a sparse graph and gradual complete extinction due to the lack of females.

Interestingly, in Run 46 (Figure 6.57) the right branch contained only a single male who, due to random chance, was not selected to mate with any of the females from the left brach, lived four years, and then died.

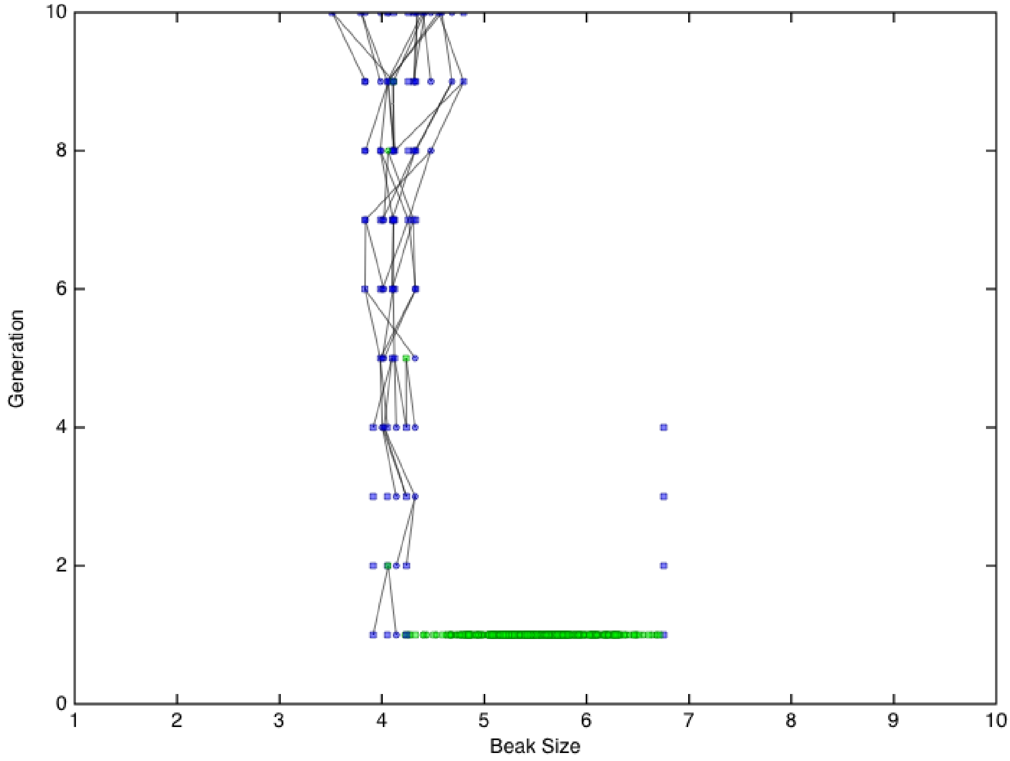

Figure 6.57: USRM, Generation 1–10, Run 46. A representative example of a population where a single male is not selected to mate with any of the females.

Generation 1–100 Plots

The first 100 generations for USRM Run 1 are shown in Figure 6.58 as a prototypical example. The defining feature for USRM is a single population, with a large amount of die-off in the center. There is also a significant random drift component. Although multiple (diffuse) green/light bars exist, branching does not occur. The average beak size can dramatically shift as seen near generation twenty.

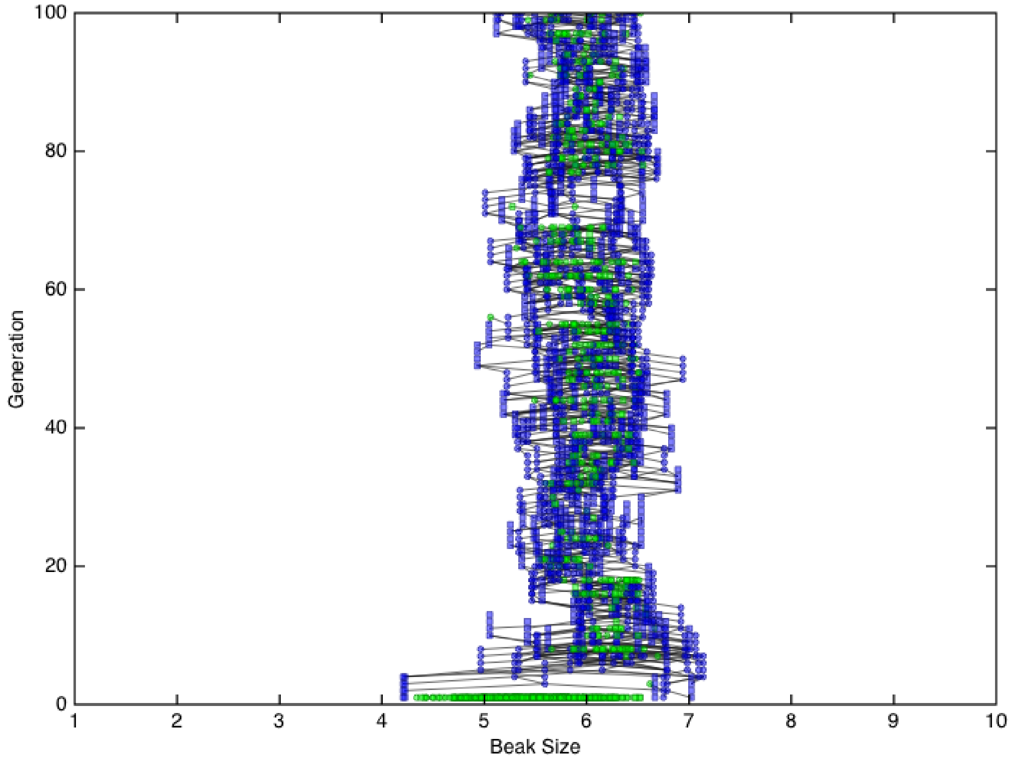

Figure 6.58: USRM, Generation 1–100, Run 1. A representative example of a single population, with a large amount of die-off in the center and a dramatic shift in the average beak size.

Extinction after generation 10 and before generation 100 is a rare event. In Run 10 (Figure 6.59), the population went extinct, terminating with a population containing only males around generation 80.

In Run 17 (see Figure 6.60), there is a significant change in the variability of the

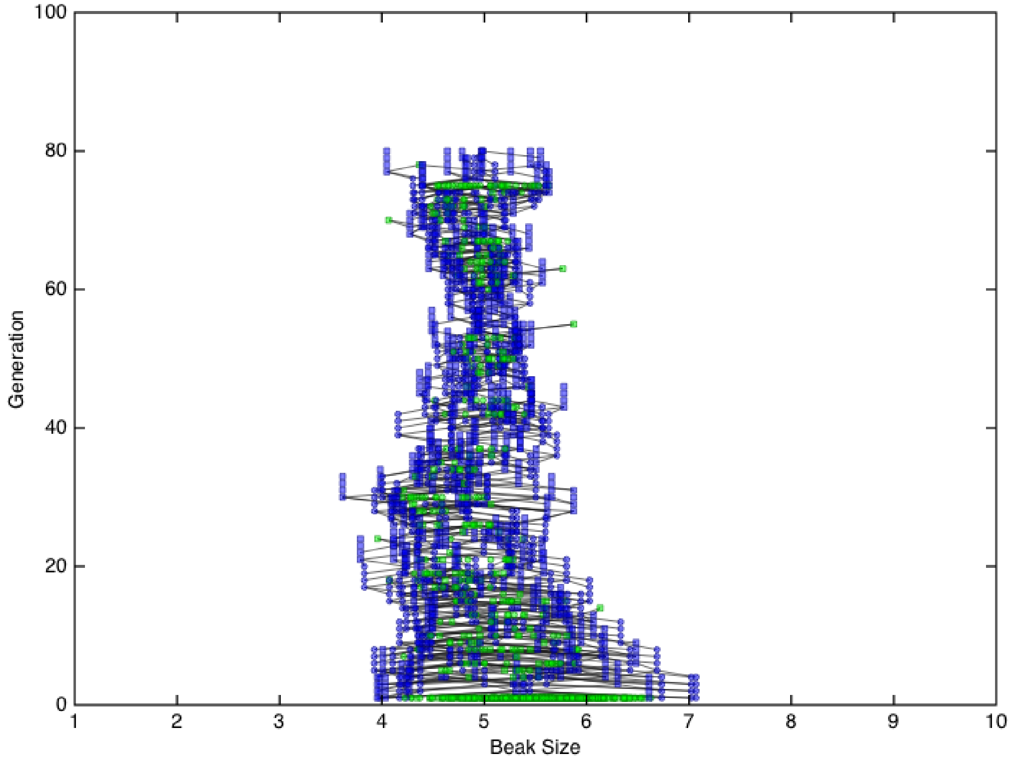

Figure 6.59: USRM, Generation 1–100, Run 10. A representative example of extinction after generation 10 and before generation 100.

population—a rapid decrease around generation 30 followed by a rapid increase.

In three repetitions (Run 1, 19 and 26) there is a significant shift in the average beak size. See Figure 6.61 for an extreme example.

In Run 20 (Figure 6.62), it appears that the population almost went extinct around generation 50 due to a bottleneck (a significant loss in variation).

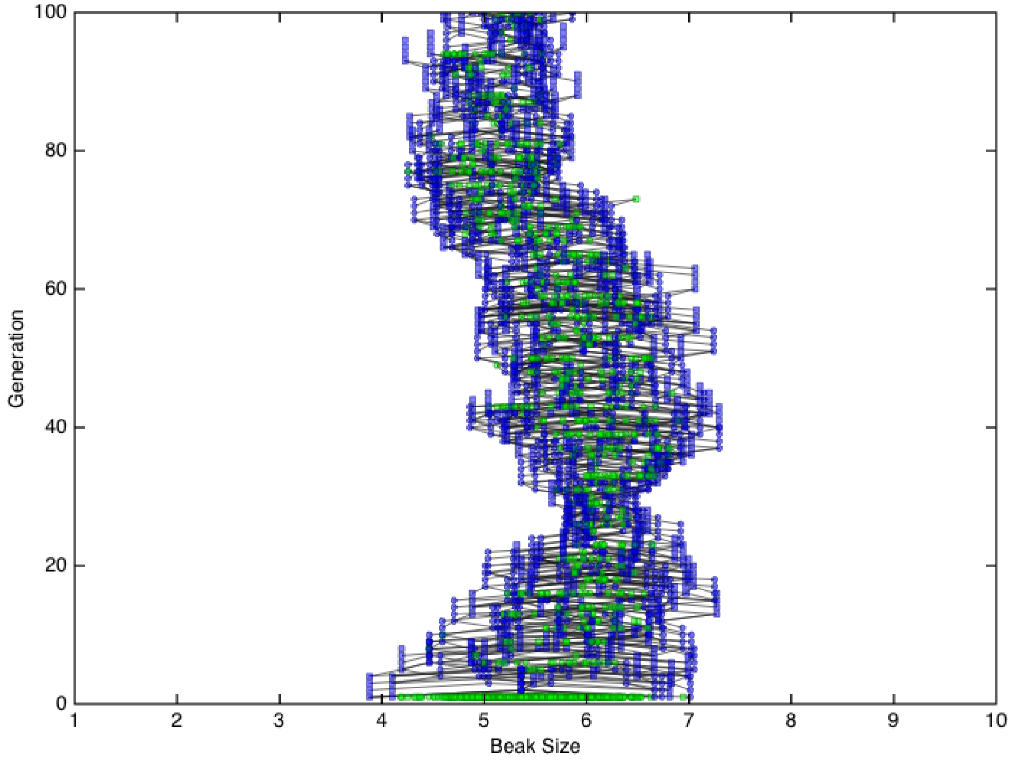

Figure 6.60: USRM, Generation 1–100, Run 17. A representative example of a significant change in the variability of the population.

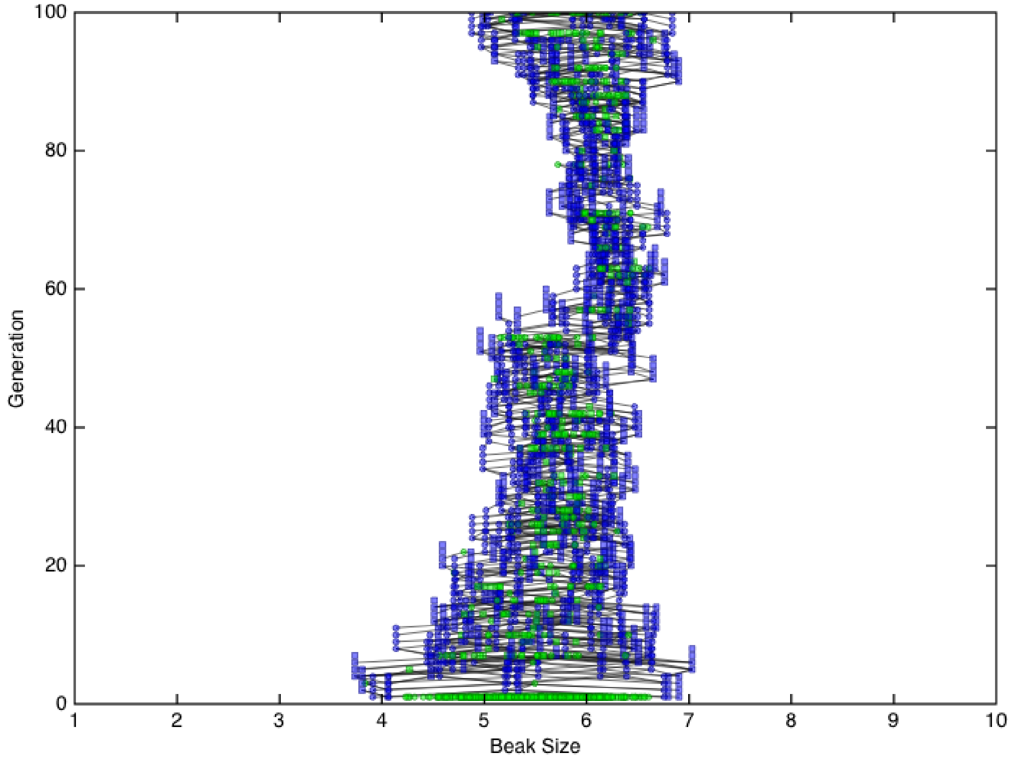

Figure 6.61: USRM, Generation 1–100, Run 19. A representative example of a significant shift in the average beak size.

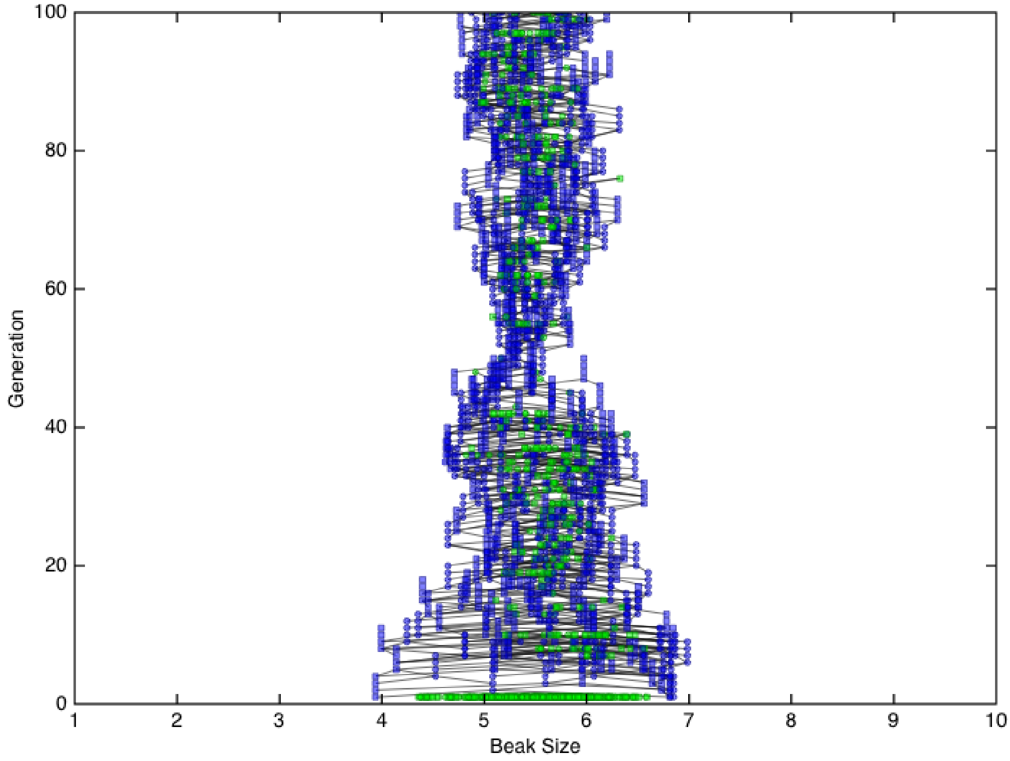

Figure 6.62: USRM, Generation 1–100, Run 20. A representative example of a bottleneck (around generation 50).

Generation 1–1000 Plots

The first 1000 generations for USRM Run 1 are shown in Figure 6.63 as a prototypical example. The defining characteristic for USRM is single population, stable up to generation 1000 with a central green/light band indicating a large die-off in the center of the population. Also, there is no branching as seen in the USAM case. Wobble in the average population beak size, a result of genetic drift, is clearly visible.

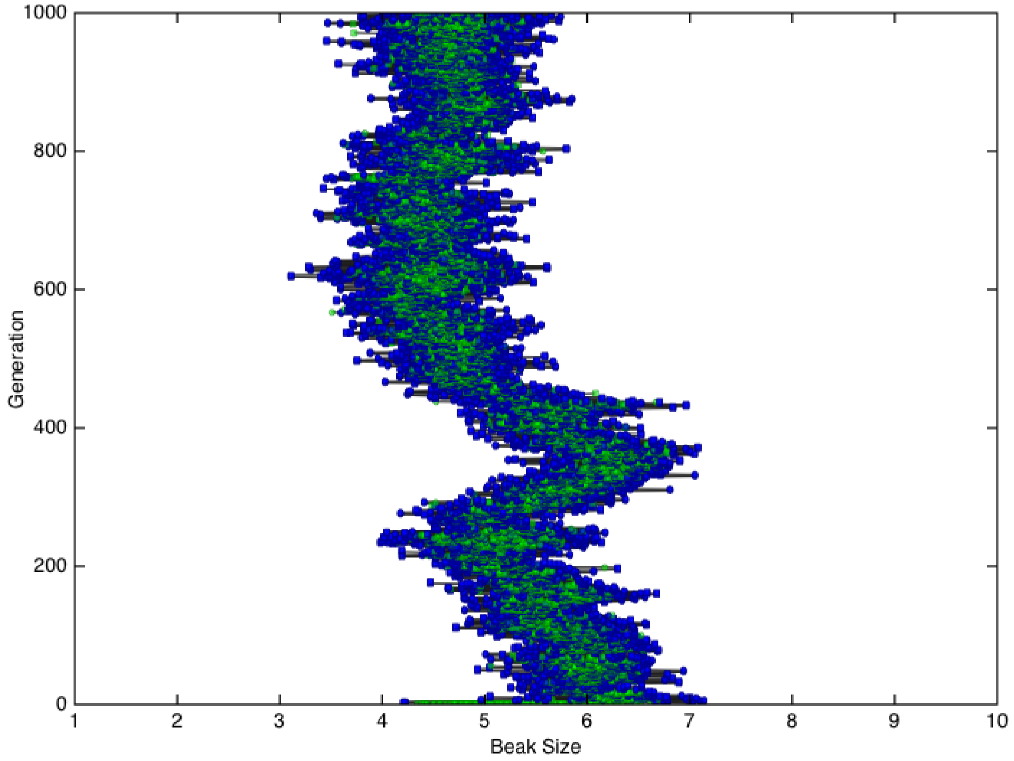

Figure 6.63: USRM, Generation 1–1000, Run 1. A prototypical example of a single population, stable up to generation 1000 with a central green/light band indicating a large die-off in the center.

Extinction after generation 100 and before generation 1000 is a rare event. In 13 repetitions (Run 5, 7, 9, 17, 23, 26, 28, 32, 34, 35, 37, 41, 46) the population went extinct due to the loss of females. See Figure 6.64 for a representative example. This is about the same number of extinctions per generation as the case for Generation 10–100 (Section 6.2.4), e.g., 13 extinctions in 900 generations averages out to 1.3 extinctions per 90 generations.

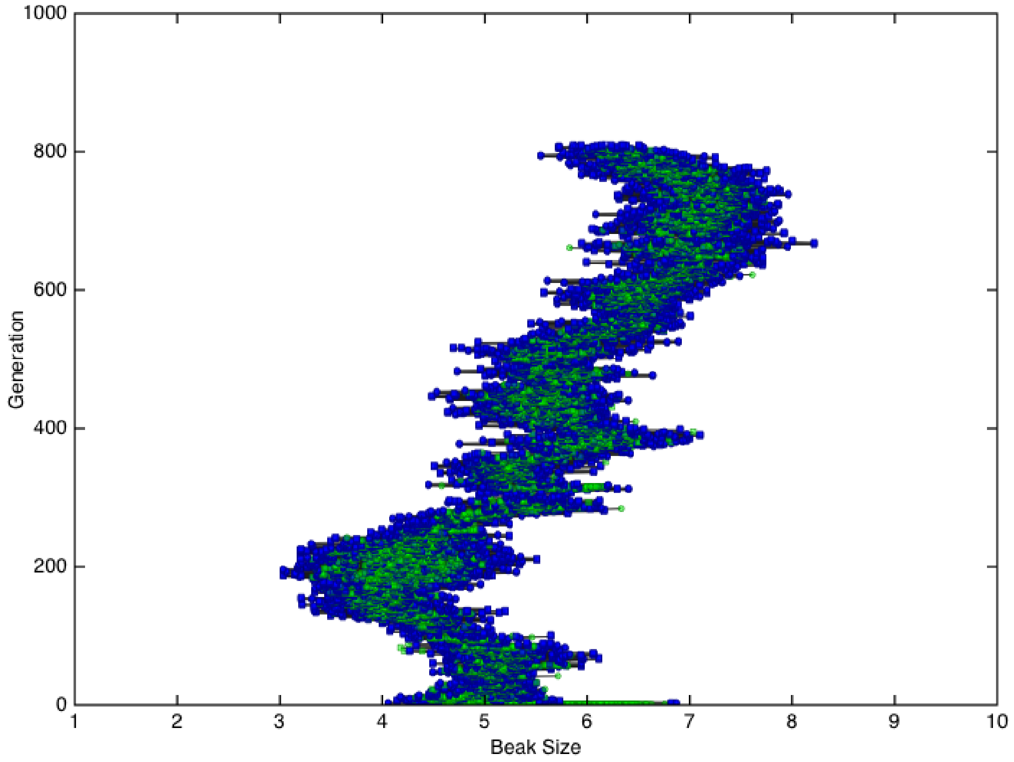

Figure 6.64: USRM, Generation 1–1000, Run 5. A representative example of extinction, after generation 100 and before generation 1000 due to the loss of females.

6.2.5 Uniform Seeds and Initial Population Die-Off

The initial beak and seed distributions for USAM, first generation before and after natural selection and beak distributions after sexual selection is shown in Figure 6.65. In the first row you can see the uniform seed distribution. There are eighteen bins with approximately 250 seeds in each for a total of around 5000 seeds. In the second row you can see the initial population distribution with mean beak size of 5.5. In the third row you can see the seed distribution after natural selection—the "center" has been carved out. In the fourth row you can see the population after natural selection—only the tails of the original distribution survive—leaving two small populations with mean beak sizes around four and seven. In the fifth row you can see the population after sexual selection and reproduction—there is a small amount of growth in the population for the smaller beak size.

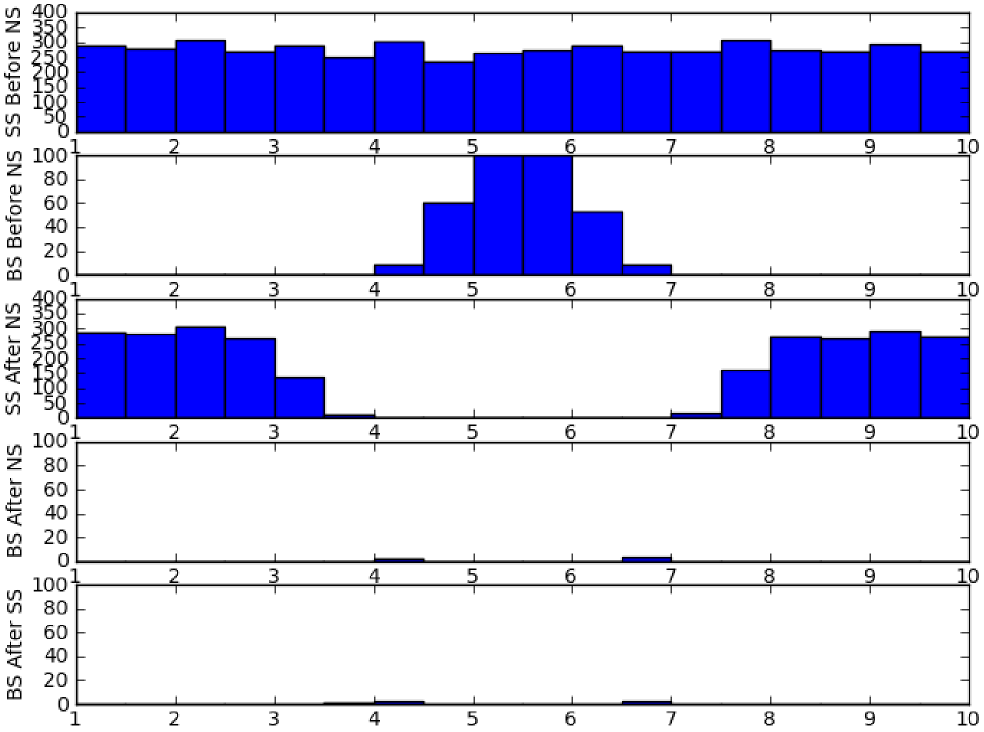

Figure 6.65: USAM, Generation 1, Run 1, population and seeds.

6.2.6 Number of Populations

The number of populations present at generation 1000 for each configuration is summarized in Table 6.1. Each column should sum to 48, the total number of repetitions for each configuration. We determined the number of populations for the final generation of each run using visual inspection. In most cases the clusters were well defined. Both cases involving random mating resulted in (at most) one population in the final generation with the uniform seeds case more likely to face extinction. Interestingly, there were no complete extinction for BSAM. The most common number of populations for USAM at generation 1000 was three. In 17 of the repetitions one of the branches went extinct, in 31 of the

Number of Populations	BSAM	BSRM	USAM	USRM
0		7	13	22
1	17	41	1	26
2	31		5	
3			19	
4			10	

Table 6.1: Number of species/populations at generation 1000 for Bimodal Seeds and Assortative Mating (BSAM), Bimodal Seeds and Random Mating (BSRM), Uniform Seeds and Assortative Mating (USAM), and Uniform Seeds and Random Mating (USRM).

	Bimodal Seeds	Uniform Seeds
Assortative Mating	0	13
Random Mating	7	22

Table 6.2: Number of complete extinction events at generation 1000.

repetition, two branches were present by the final generation.

6.2.7 Complete Extinction Events

Observe the number of populations in the first row of Table 6.1. This is the number of complete extinctions for each configuration. Complete extinction can take place at the very start the simulation during natural selection (false starts) or any time thereafter. The number of complete extinctions for the four datasets, generation 1–1000, is shown in Table 6.2. The number of complete extinctions not due to false starts (see Section 6.2.8) is shown in Figure 6.3.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	0	2
Random Mating	7	17

Table 6.3: Number of complete extinction events at generation 1000 not due to false starts.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	0	11
Random Mating	0	5

Table 6.4: Number of false starts.

6.2.8 False Starts

The number of false starts for each configuration is shown in Table 6.4. A false start is a complete extinction in which no breeding takes place. This can be due to initial conditions or behavior. In this case, complete extinction will occur within the first four generations/years which is the lifespan of an individual.

False starts due to initial conditions, shown in Figure 6.5, occur when the entire population (both the left and right branches) contain individuals of a single gender. For example USAM Run 5 (Figure 6.35) contains only males, and USAM Run 45 (Figure 6.37) contains

	Bimodal Seeds	Uniform Seeds
Assortative Mating	0	6
Random Mating	0	5

Table 6.5: Number of false starts due to initial conditions.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	0	5
Random Mating	0	0

Table 6.6: Number of false starts due to behavior.

only females. Note that the false starts appear to be associated with the uniform seeds case.

False starts due to behavior, shown in Figure 6.6, occur when one branch contains all females, the other branch contains all males, and the females refuse to pick males from the other branch even though they face extinction. This can not occur for the random mating case (bottom row) because females, in this situation, will always pick a random male from the other branch. Interestingly, the BSAM case has no extinctions. The only configuration with false starts of this type is USAM (Run 6, 38, 39, 46, 47). For example, USAM Run 6 (Figure 6.42) contains a single male in the left branch and only females in the right branch.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	10.9	5.67
Random Mating	11.3	5.96

Table 6.7: Initial population size after natural selection at first generation.

6.2.9 Initial Population Size

The average initial population size (after natural selection) for the 48 repetitions is shown in Figure 6.7. The values in each column are approximately the same because each column has the same initial seed distribution. The bimodal seeds case has a population size which is almost twice as large as the uniform seeds case. This is because of the different overlap between the initial population distribution and the given seed distribution. This larger population size is why the number of false starts due to initial conditions is zero for the bimodal seeds case in Table 6.5—there is a threshold for the population size with respect to initial population stability. The larger population size for the bimodal seeds case is also responsible for lack of false starts due to behavior in the BSAM case (see Table 6.6). If the initial population sizes were the same we would expect to see the same number as found in the USAM case.

6.2.10 Average Number of Populations

The average number of populations without extinctions is the number of populations you would expect to find in the last generation if the entire population did not go extinct.

The average number of populations at generation 1000, averaged over each of the 48

	Bimodal Seeds	Uniform Seeds
Assortative Mating	1.65	2.25
Random Mating	0.854	0.542

Table 6.8: Average number of populations.

repetitions, is shown in Table 6.8 (with extinctions) and Table 6.9 (without extinctions).

For each case in which extinctions are included, the weighted sum for a given column in Table 6.1 is divided by 48 (the sum of all rows for a column). In each case in which extinctions are not included, the weighted sum is divided by the sum of all rows for a given column except for the first row. For the BSAM case, the number including and excluding extinctions is the same because there are no extinctions. For all the other cases, the average number of populations including extinctions is lower. In both cases involving random mating, you would expect to see a single population. For the USAM case, you would expect to see around three populations. For the BSAM case you would expect to see at least one population.

6.2.11 Average Population Size

The average population size for the entire population, computed with and without extinction events is shown in Table 6.10 and 6.11.

The average population size is found by summing the population size for each repetition in a given dataset at generation 1000 after natural selection. This sum is then normalized by the total number of repetitions (48) resulting in the average size. For the average without extinction events, the sum is normalized by the total number of repetitions which did not

	Bimodal Seeds	Uniform Seeds
Assortative Mating	1.65	3.09
Random Mating	1.0	1.0

Table 6.9: Average number of populations without extinctions.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	43.5	32.3
Random Mating	21.7	9.90

Table 6.10: Average population size after natural selection at generation 1000.

result in extinction.

The average total population size, excluding extinctions, for the USAM case is larger (41.31) than the USRM case (18.4). After considering the average number of populations in each case, the average subpopulation size for the USAM (13.4) case is actually smaller than the USRM (18.4) case.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	43.5	41.31
Random Mating	26.0	18.4

Table 6.11: Average population size without extinction events after natural selection at generation 1000.

6.3 10x Seeds

The section includes the results for the BSAM, BSRM, USAM, and USRM configurations for the case when there are 50000 (10x) seeds. Here 24 repetitions were completed for each case, rather than 48. Population graphs are shown along with quantitative results detailing the average population size.

6.3.1 Bimodal Seeds & Assortative Mating

The results for BSAM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for BSAM Run 1 are shown in Figure 6.66 as a prototypical example. The results are very similar to the 1x case except there are more individuals. Unlike the 1x case both branches remained stable up to generation 10. Interestingly, in one repetition (Run 8, Figure 6.67), two individuals from the inner edge of each branch (at generation two) produce an (inviable) offspring. Conversely, the 1x case produced no hybrid offspring.

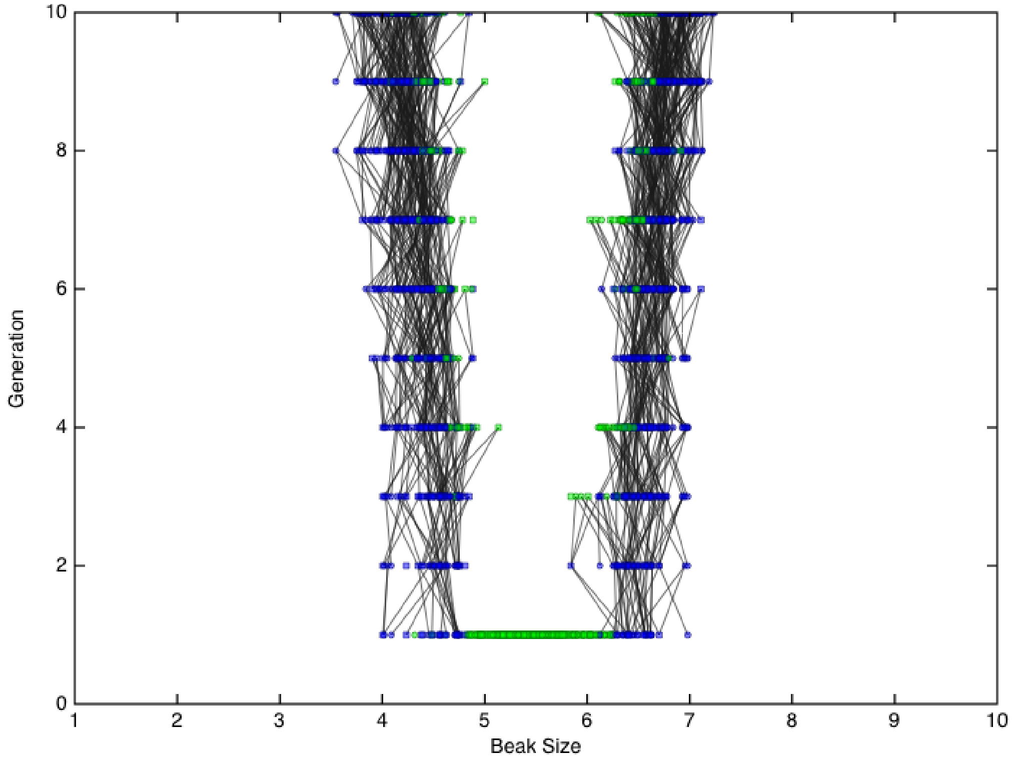

Figure 6.66: 10x Seeds, BSAM, Generation 1–10, Run 1. A representative example of a population with two non-interbreeding branches.

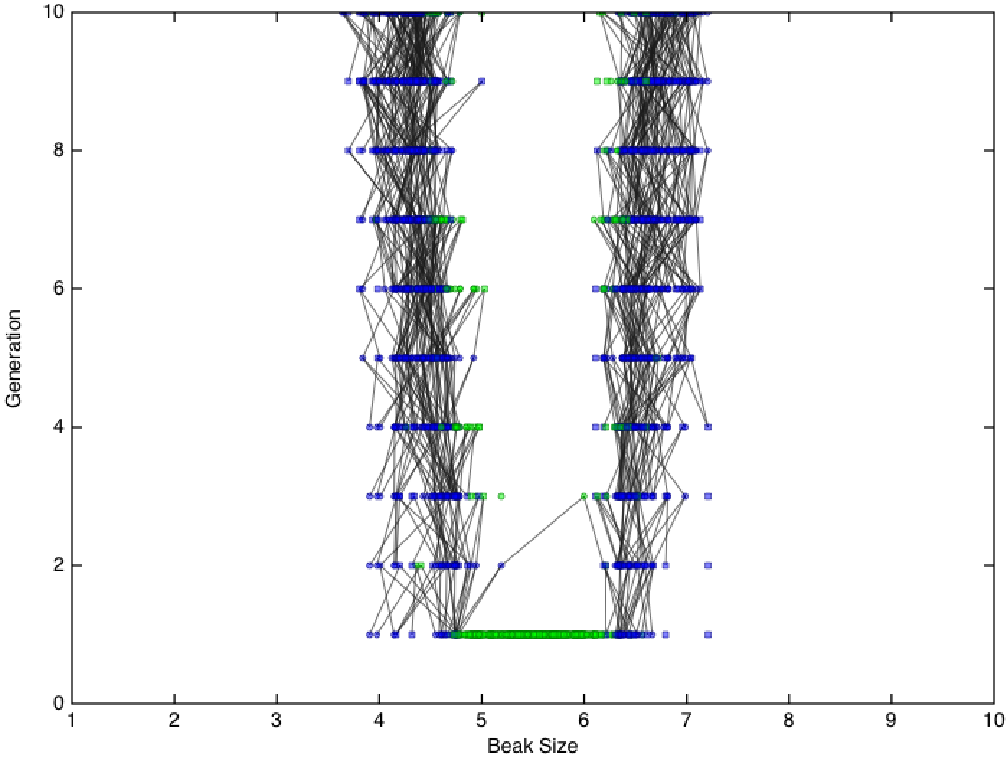

Figure 6.67: 10x Seeds, BSAM, Generation 1–10, Run 8. A single example of a hybrid offspring.

Generation 1–100 Plots

The first 100 generations for BSAM Run 1 are shown in Figure 6.68 as a prototypical example. The results for the 10x case is very similar to the 1x case except there are more individuals. The horizontal banding seen in the 1x case is still present. As in the 1x case, there is a large initial die-off. However, it is not as intense—more of the individuals (in an absolute sense) are surviving at the tails.

The die-off near the inner edge of each branch is similar to the 1x seed case—becoming more diffuse by generation forty. There is also a slight reduction in the number of extinctions after generation 10 and before generation 100. The number of extinctions is zero compared to one for the 1x case. The width of each branch is larger due the increased availability of seeds.

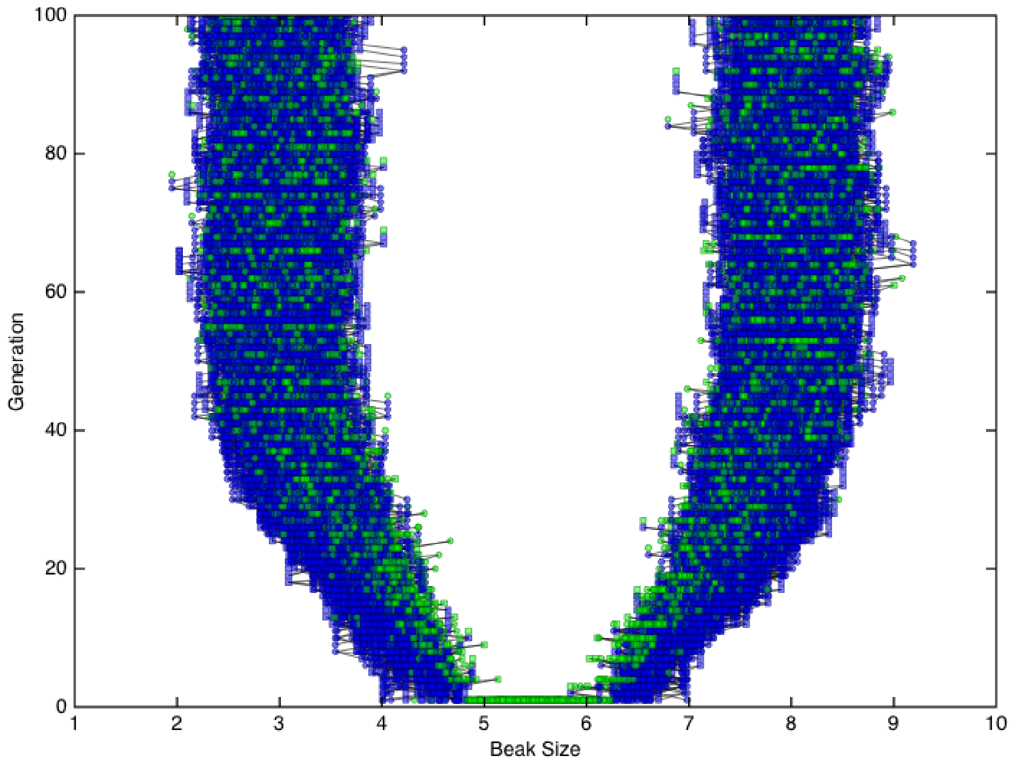

Figure 6.68: 10x Seeds, BSAM, Generation 1–100, Run 1. A representative example of a population with two non-interbreeding branches.

Generation 1–1000 Plots

The first 1000 generations for BSRM Run 1 are shown in Figure 6.69 as a prototypical example. The results are very similar to the 1x case except the branches are wider due to the increased availability of seeds. There are no branch extinctions after generation 100 and before generation 1000, as in the 1x case. The 10x seed case was highly stable. In all 24 repetitions both branches were present in the last generation.

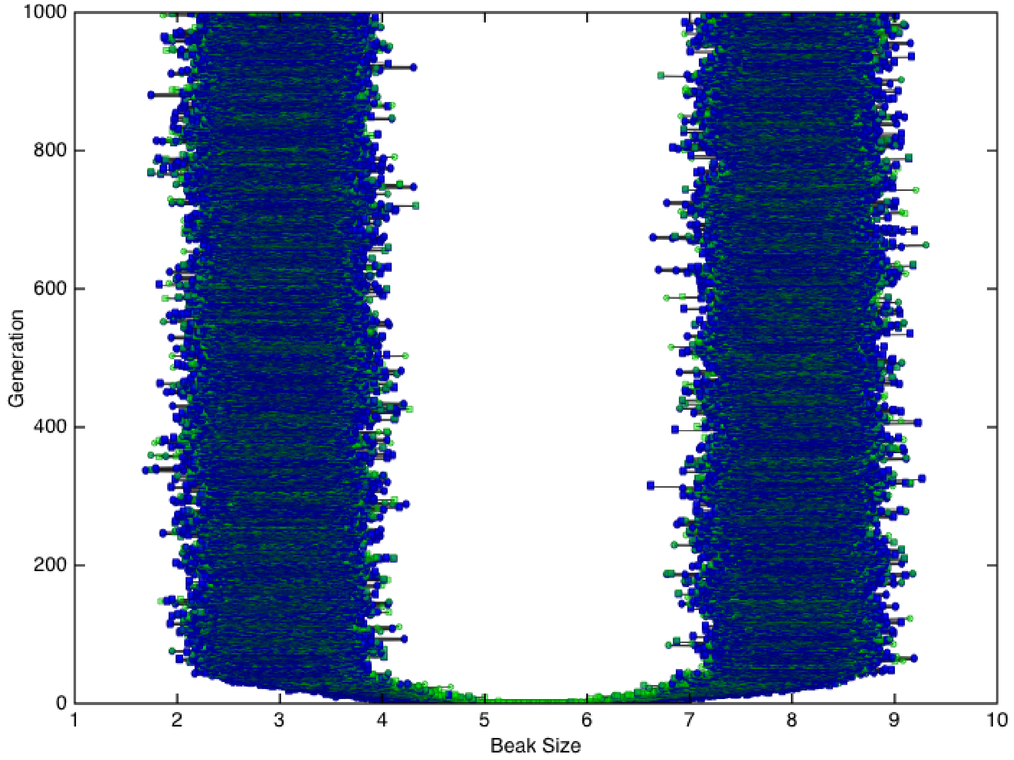

Figure 6.69: 10x Seeds, BSAM, Generation 1–1000, Run 1. A representative example of a population with two non-interbreeding branches.

6.3.2 Bimodal Seeds & Random Mating

The results for BSRM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for BSRM Run 1 are shown in Figure 6.70 as a prototypical example. The results for the 10x case are very similar to the 1x case except there is a significant increase in the number of individuals in each branch along with the number of inviable offspring. Unlike the 1x seed case there are no branch extinctions, both branches remain stable up to generation 10. The initial die-off is not as severe as the 1x case—more individuals (in an absolute sense) survive near the tails of the initial population.

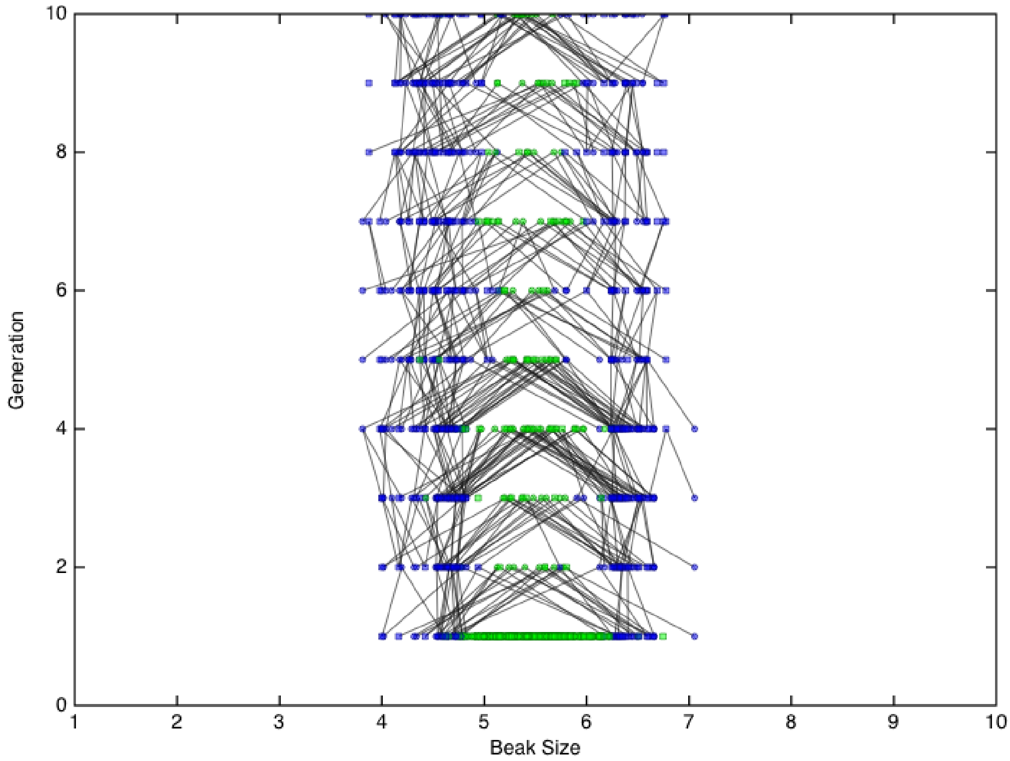

Figure 6.70: 10x Seeds, BSRM, Generation 1–10, Run 1. A representative example of population with two interbreeding branches.

Generation 1–100 Plots

The first 100 generations for BSRM Run 1 are shown in Figure 6.71 as a prototypical example. The results are very similar to the 1x case except there are more individuals and better branch stability. The number of populations at generation 100 is one, as the 1x case. At most one population is supported due to left extinction (for example, Run 9, Figure 6.72) or right extinction (for example, Run 1, Figure 6.71). Interestingly, it appears that the 10x case is supporting two populations for a larger number of generations. An extreme case is Run 9 (Figure 6.72) where two populations were supported past generation 50. Unlike the 1x case, there are no complete extinctions.

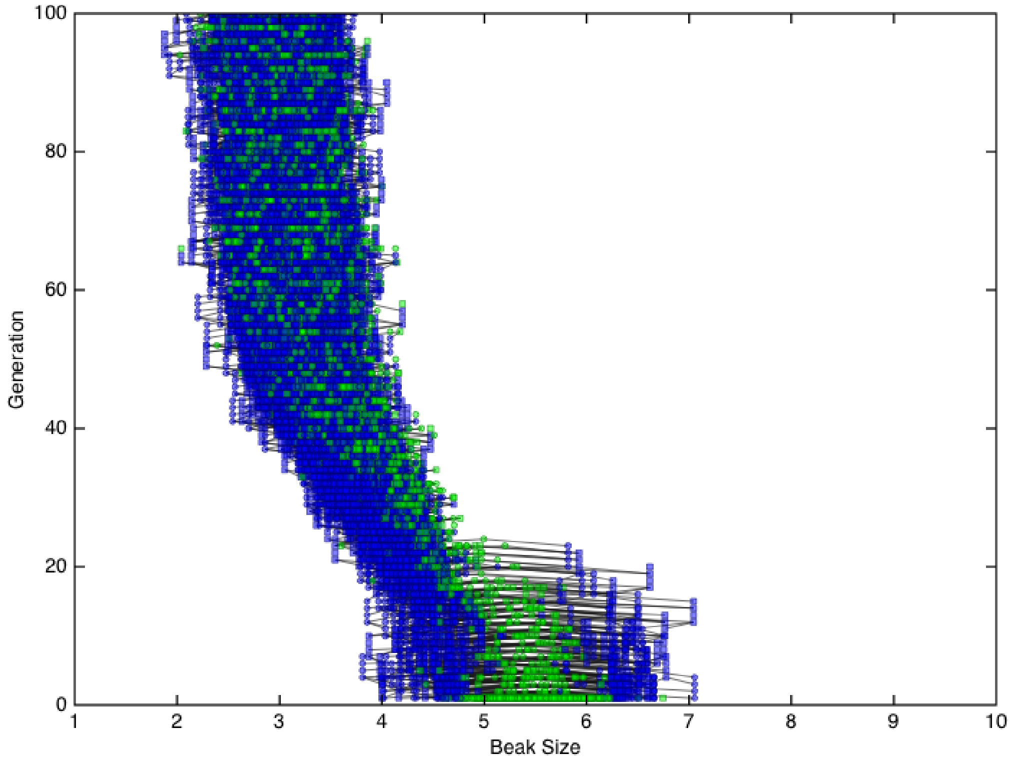

Figure 6.71: 10x Seeds, BSRM, Generation 1–100, Run 1. A representative example of right branch extinction.

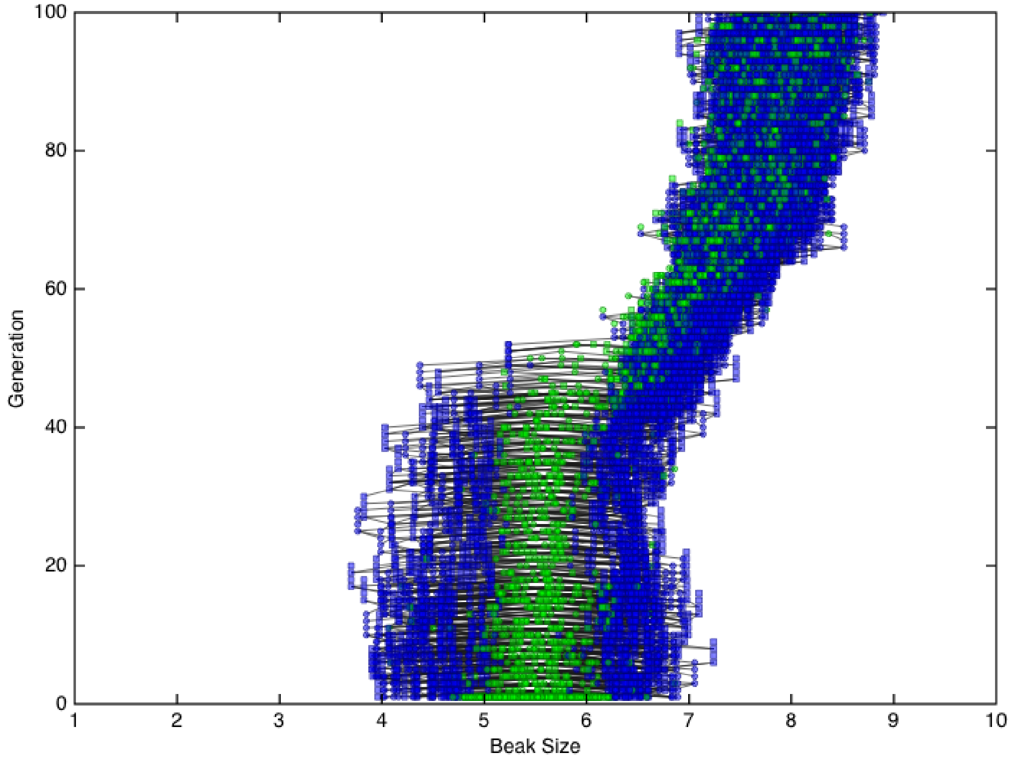

Figure 6.72: 10x Seeds, BSRM, Generation 1–100, Run 9. A representative example of a population supporting two populations past generation 50 with eventual left branch extinction.

Generation 1–1000 Plots

The first 1000 generations for BSRM Run 1 are shown in Figure 6.73 as a prototypical example. The results are very similar to the 1x case except there is a significant increase in the number of individuals in each branch. At most one population is supported at generation 1000 due to left extinction (for example, Run 3, Figure 6.74) or right extinction (for example, Run 1, Figure 6.73), as in the 100 Generation case. There are no complete extinctions before generation 1000.

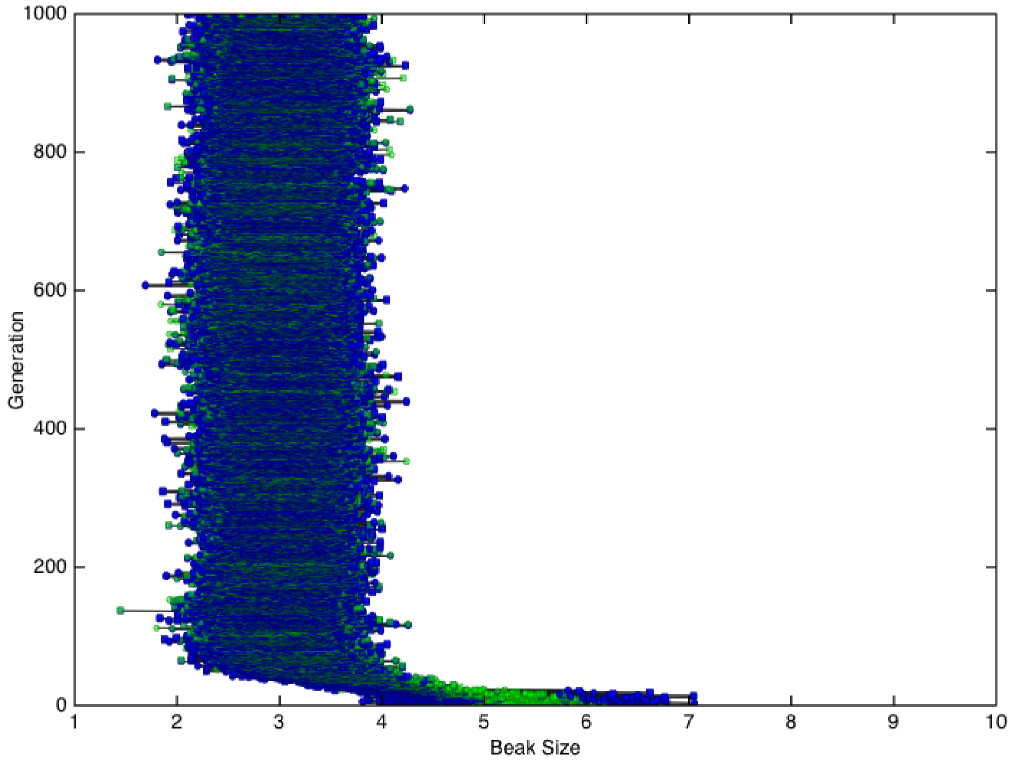

Figure 6.73: 10x Seeds, BSRM, Generation 1–1000, Run 1. A representative example of right branch extinction.

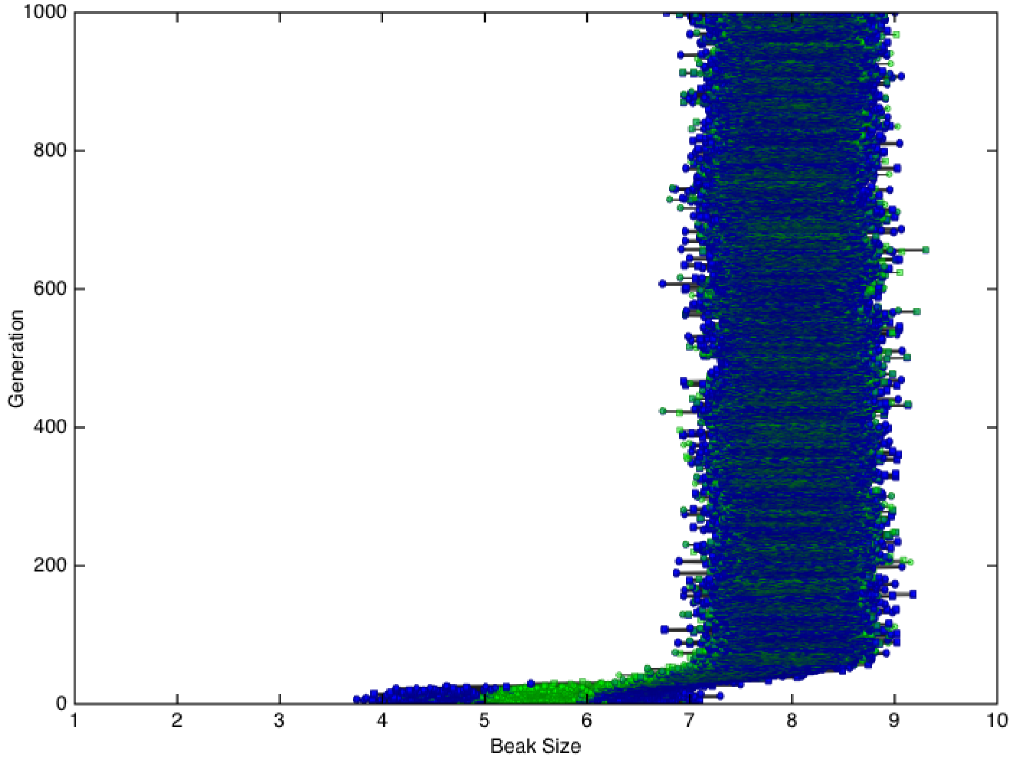

Figure 6.74: 10x Seeds, BSRM, Generation 1–1000, Run 3. A representative example of left branch extinction.

6.3.3 Uniform Seeds & Assortative Mating

The results for USAM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for USAM Run 1 are shown in Figure 6.75 as a prototypical example. The results are clearly different than the 1x case. First, there is not a clear distinction between the left and right branches due to the significant amount of interbreeding. Second, the stability of the two branches is dramatically increased due to the larger population size.

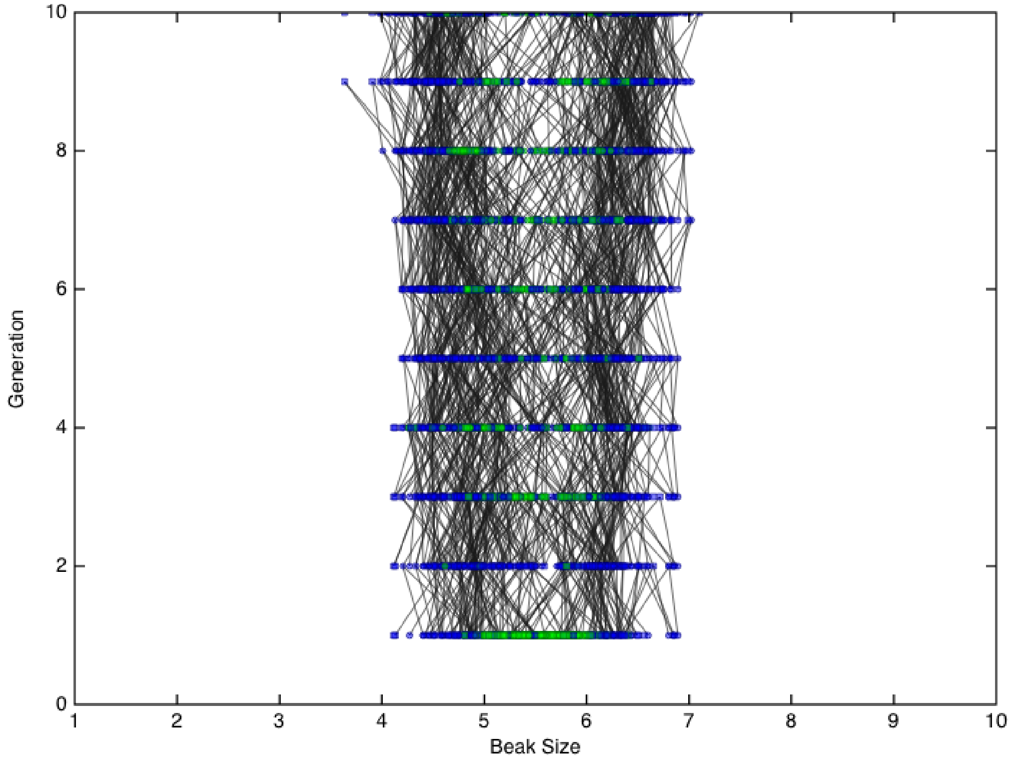

Figure 6.75: 10x Seeds, USAM, Generation 1–10, Run 1. A representative example of population with two highly interbreeding branches.

Generation 1–100 Plots

The first 100 generations for USAM Run 1 are shown in Figure 6.76 as a prototypical example. The results are significantly different than the 1x case. The branching structure is more regular and symmetric than the 1x case. The amount of symmetry did vary from high (for example, Run 8, Figure 6.77) to medium (for example, Run 1, Figure 6.76), to low (for example, Run 2, Figure 6.78). The number of branches at generation 100 is limited to three (for example, Run 2, Figure 6.78) or four (for example, Run 1, Figure 6.76). In some cases the number of species is not clear (for example, Run 6, Figure 6.79). Interestingly, the center can be repopulated after an initial split (for example, Run 2, Figure 6.78).

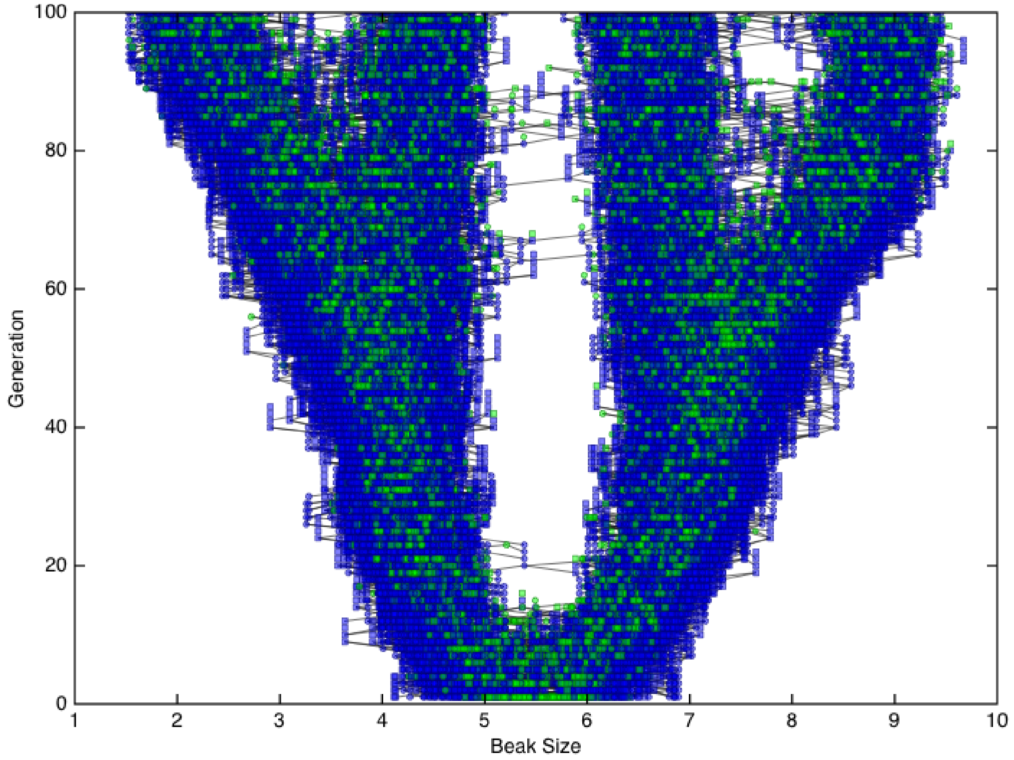

Figure 6.76: 10x Seeds, USAM, Generation 1–100, Run 1. A representative example of a population with medium symmetry and four species at generation 100.

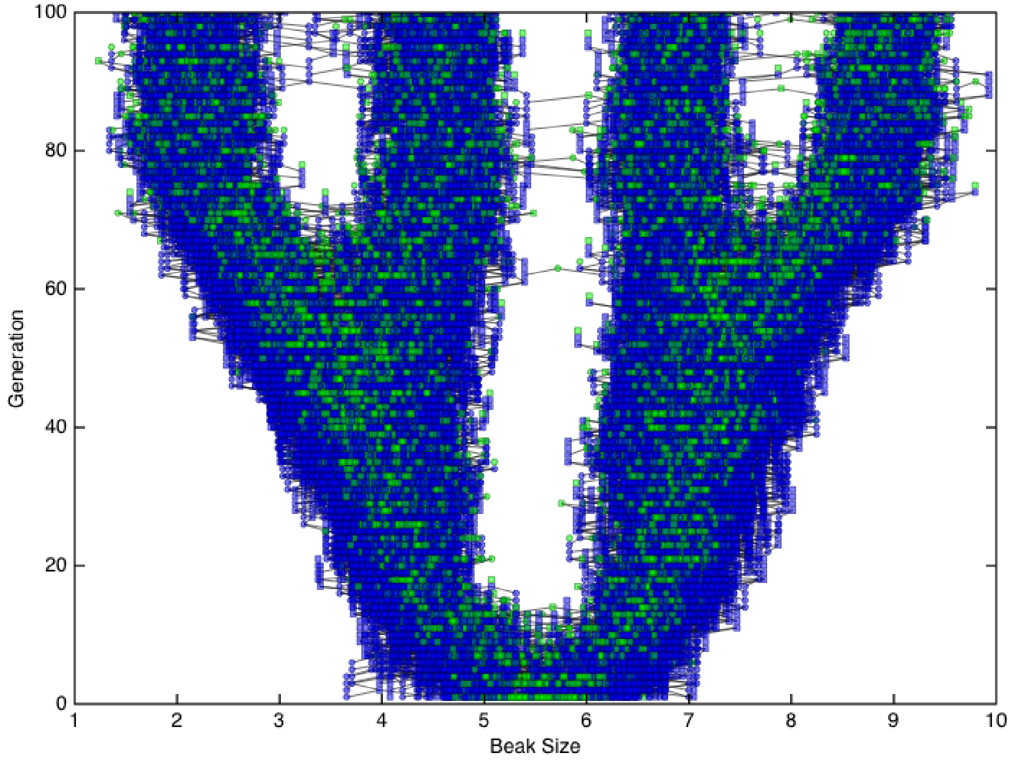

Figure 6.77: 10x Seeds, USAM, Generation 1–10, Run 8. A representative example of a population with high symmetry.

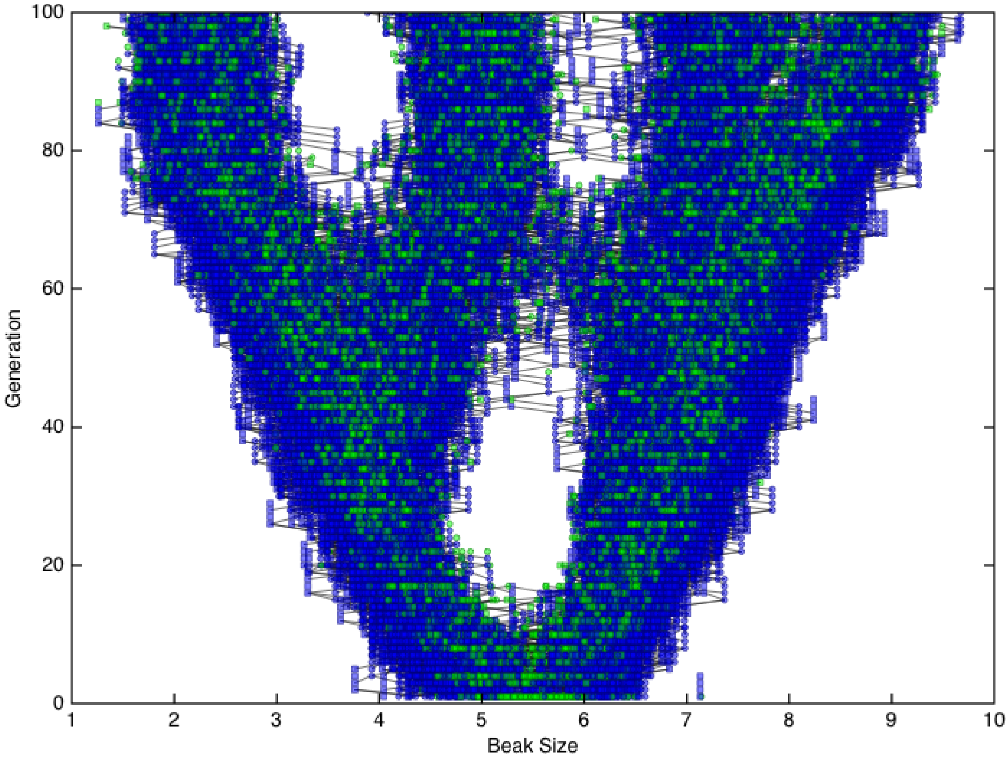

Figure 6.78: 10x Seeds, USAM, Generation 1–10, Run 2. A representative example of a population with low symmetry and three species at generation 100 with the center repopulated.

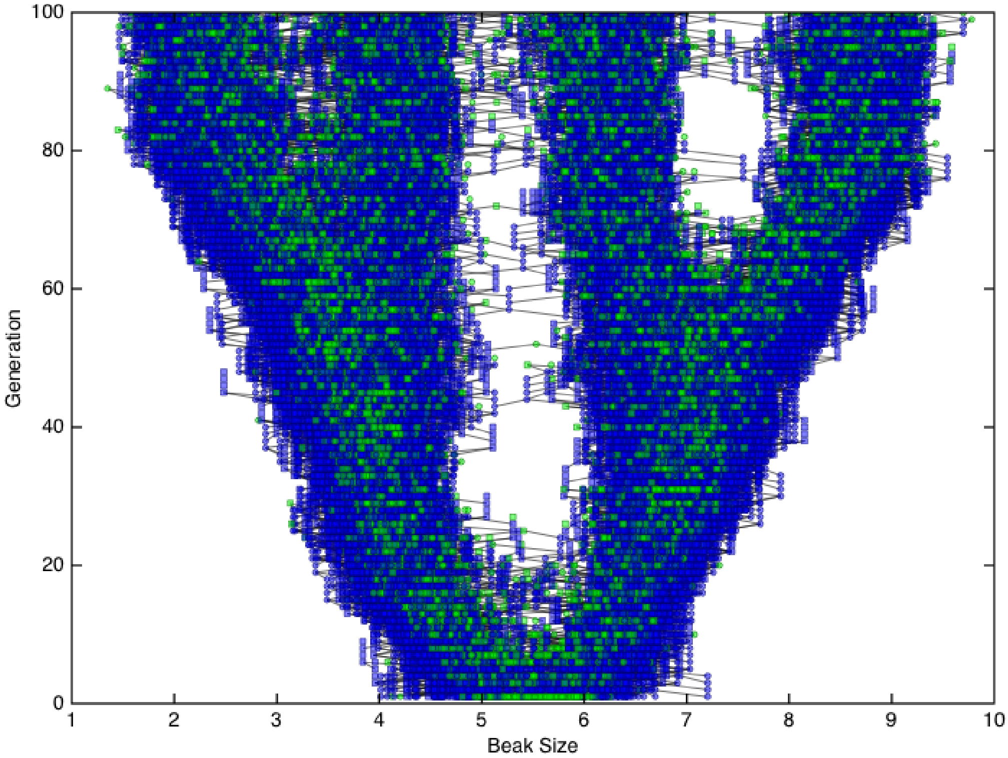

Figure 6.79: 10x Seeds, USAM, Generation 1–10, Run 6. A representative example of a population where the number of species at generation 100 is not clear.

Generation 1–1000 Plots

The first 1000 generations for USAM Run 1 are shown in Figure 6.80 as a prototypical example. The results are clearly different than the 1x case. The chaotic branching and merging found in the corresponding 1x case is absent. Instead, four populations are formed around generation 100 and remain stable up to generation 1000. A significant amount of interbreeding takes place between the adjacent branches. See Run 24 (Figure 6.81) for an example of intense hybridization between the center branches.

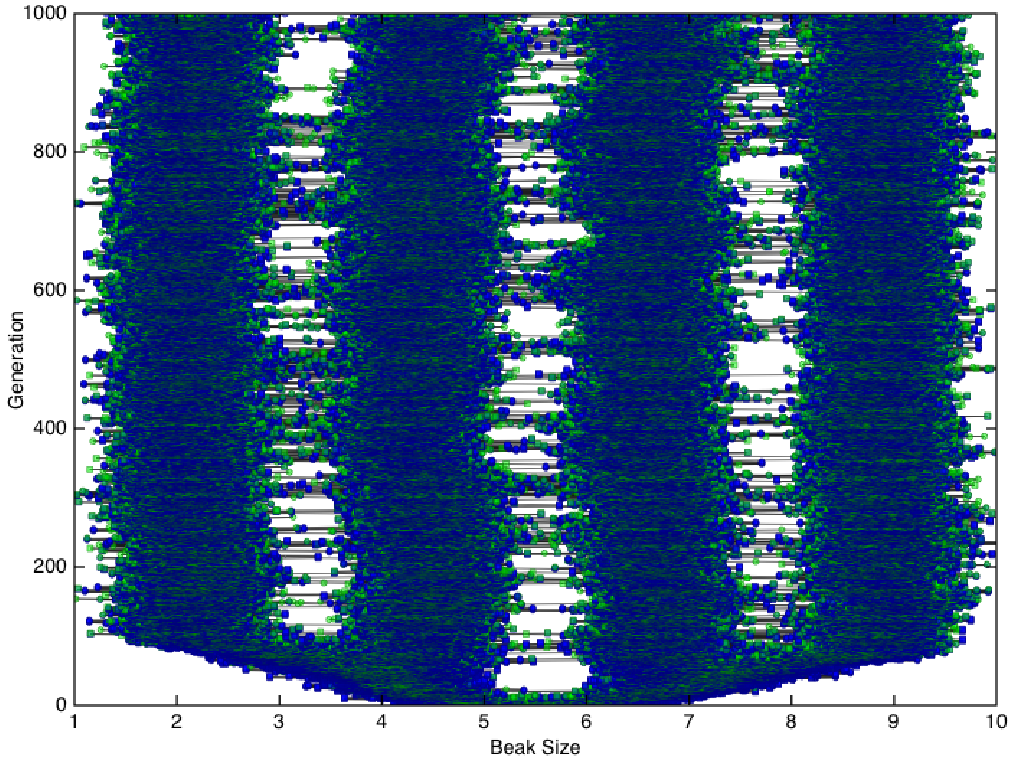

Figure 6.80: 10x Seeds, USAM, Generation 1–1000, Run 1. A representative example of a population with four branches with significant interbreeding.

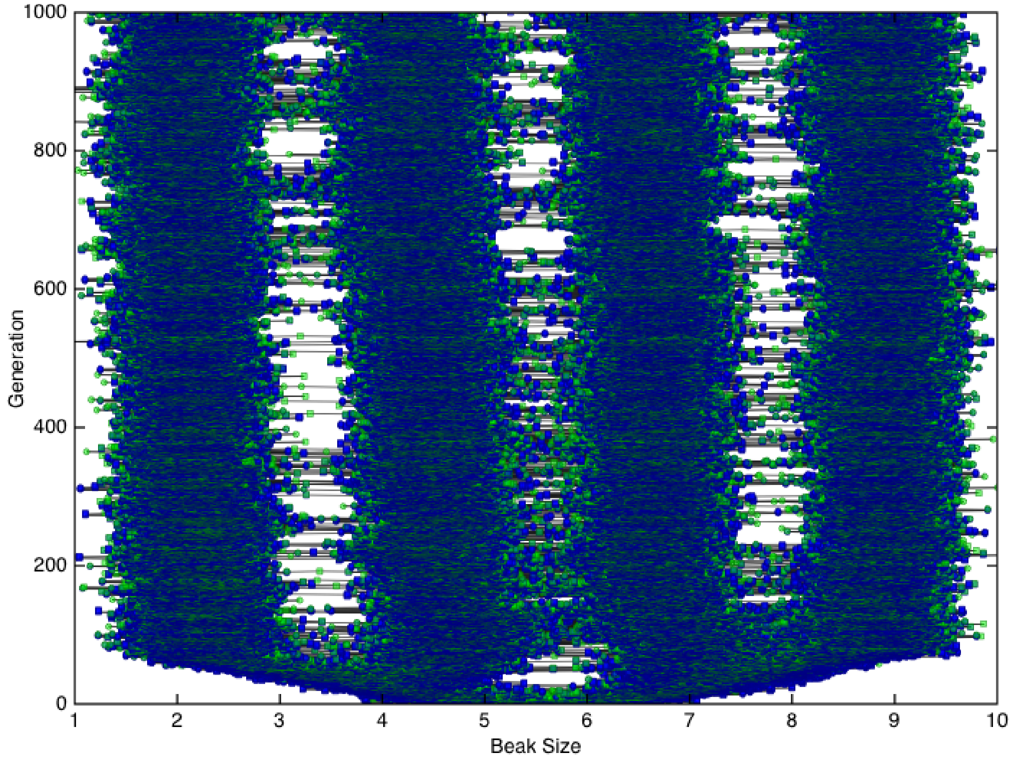

Figure 6.81: 10x Seeds, USAM, Generation 1–1000, Run 24. A representative example of a population with four branches with intense hybridization (between the center branches).

6.3.4 Uniform Seeds & Random Mating

The results for USRM are shown for the first 10, 100, and 1000 generations.

Generation 1–10 Plots

The first 10 generations for USRM Run 1 are shown in Figure 6.82 as a prototypical example. The results are similar to the 1x case, except that the population is significantly larger. As with the 1x case, there is a single population with a periodic die-off in the center. For example, there is a large die-off in generations 1, 3 and 6.

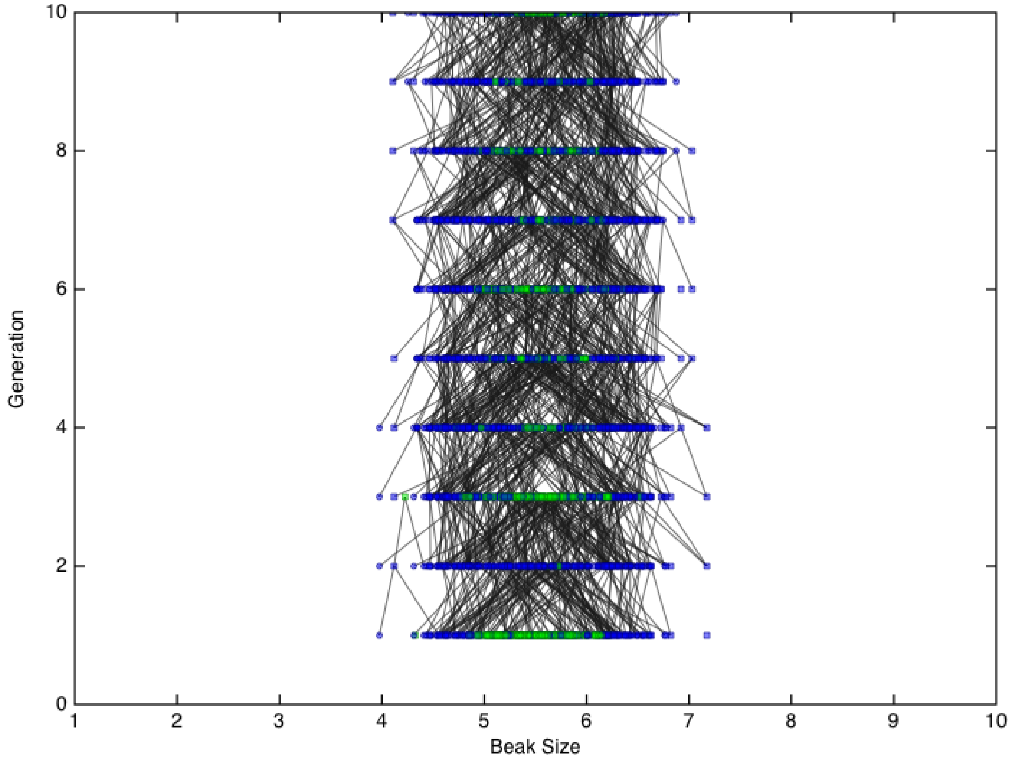

Figure 6.82: 10x Seeds, USRM, Generation 1–10, Run 1. A representative example of a single interbreeding population with periodic die-off in the center.

As with the USAM case, the initial die-off is not as intense as it is in the 1x case. The population size is larger but otherwise the results are unchanged.

Generation 1–100 Plots

The first 100 generations for USRM Run 1 are shown in Figure 6.83 as a prototypical example. The results are similar to the 1x case: a single population with a significant die-off in the center. Green/light banding, composed of sparse or sometimes dense green/light bars, is clearly visible due to the larger population size.

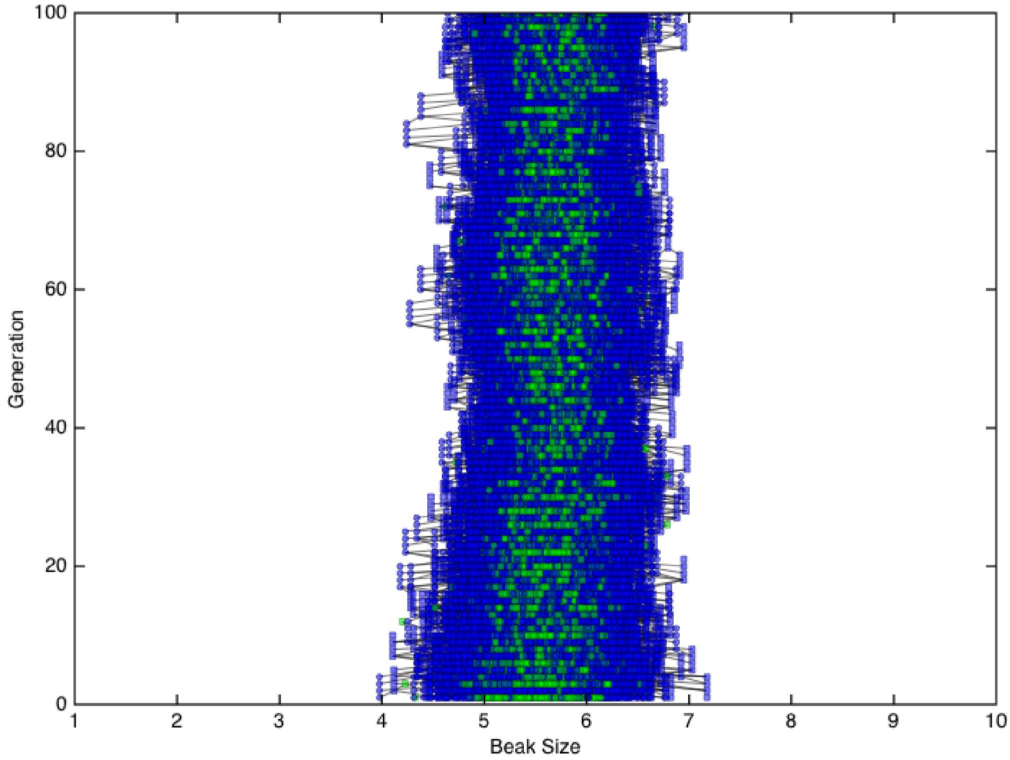

Figure 6.83: 10x Seeds, USRM, Generation 1–100, Run 1. A representative example of a single interbreeding population with significant die-off in the center.

Generation 1–1000 Plots

The first 1000 generations for USRM Run 1 are shown in Figure 6.84 as a prototypical example. The results are similar to the 1x case, a single population with a significant die-off in the center. Overall, the genetic drift component appears to be significantly reduced due to the increased population size. There remain isolated cases of sustained drift (see Run 20, Figure 6.85).

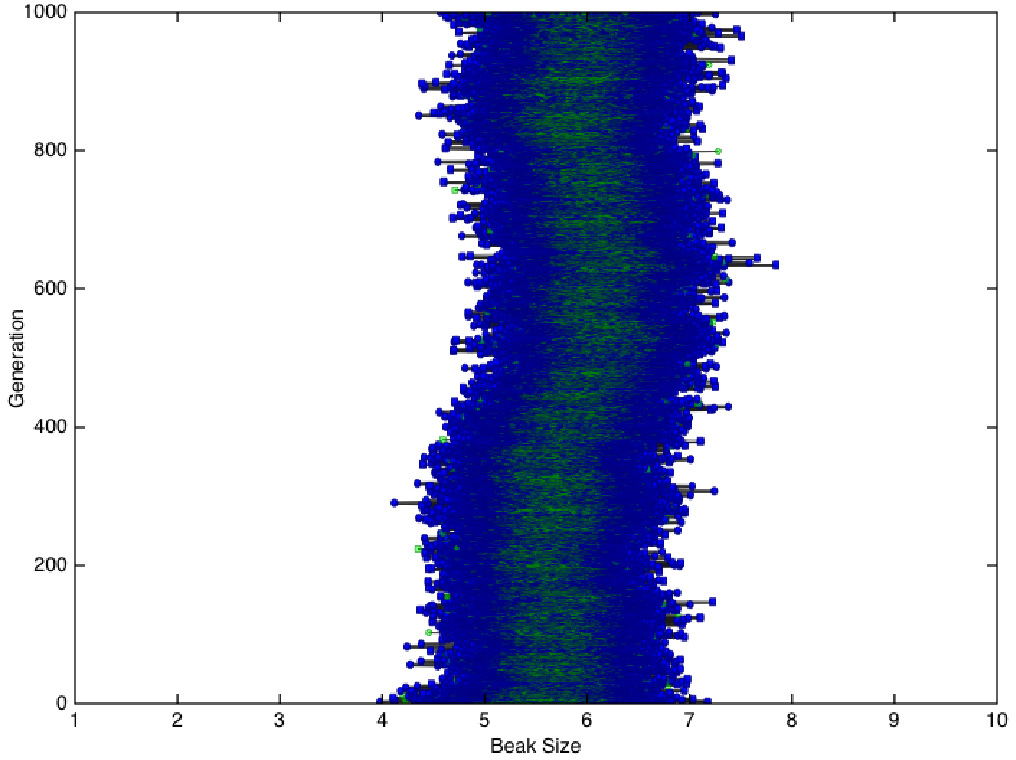

Figure 6.84: 10x Seeds, USRM, Generation 1–1000, Run 1. A representative example of a single interbreeding population with genetic drift.

6.3.5 Initial Population Size

The average population size after natural selection at the first generation are shown in Table 6.12. The values in each column are about the same (they both have the same eed

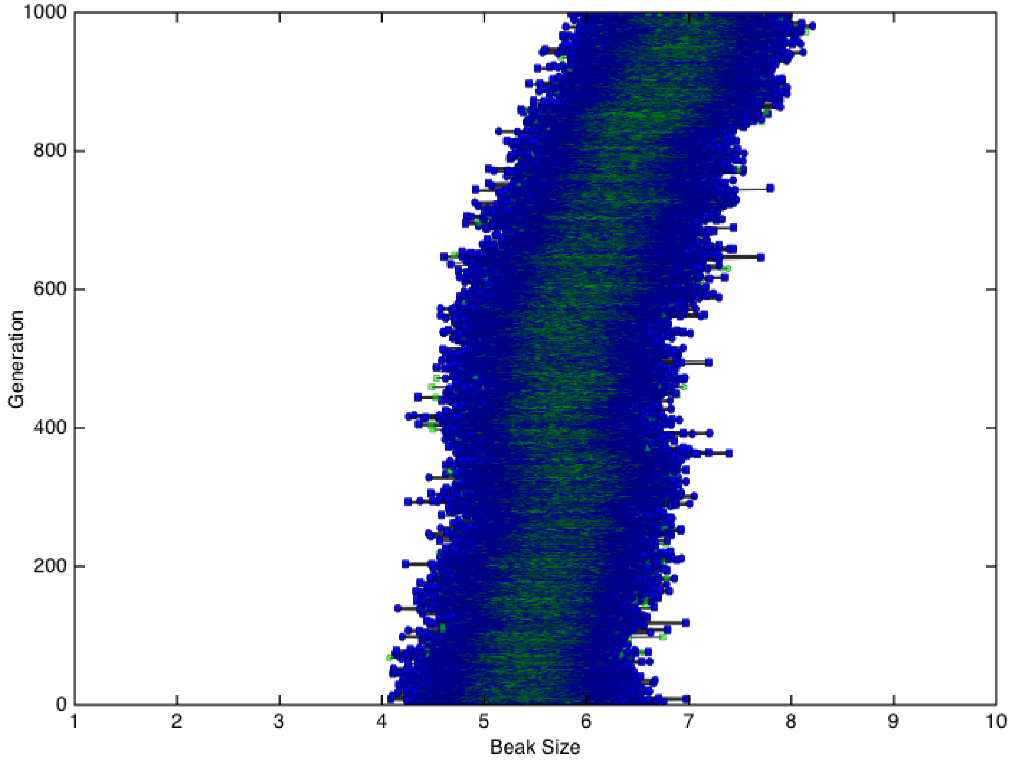

Figure 6.85: 10x Seeds, USRM, Generation 1–1000, Run 20. A representative example of a single interbreeding population with sustained genetic drift.

distribution). For the bimodal seed case, the population was roughly five times larger than the 1x case (see Table 6.7). This is due to the partial overlap of the initial population and the seed distributions. The more interesting case is uniform seeds. Here, the population was nearly 25 times larger for a 10 times increase in seeds.

6.3.6 Average Population size

The average population sizes values after natural selection at generation 1000 are shown in Table 6.13. Recall that there were no extinctions in the 10x case. Compared to the results for the 1x case without extinctions (See Table 6.11) the average population size for each configuration is roughly 10 times larger than the 1x case. This means that the population size is roughly proportional to the seeds available as expected.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	48.2	139
Random Mating	51.5	140

Table 6.12: Average population size after natural selection at the first generation.

	Bimodal Seeds	Uniform Seeds
Assortative Mating	541	546
Random Mating	280	208

Table 6.13: Average population size after natural selection without extinctions at generation 1000.

CHAPTER 7

Discussion

The results provide direct evidence for the proposed hypotheses and some surprising outcomes that we did not anticipate, in particular emergent phenomena.

In the data collected we found speciation for bimodal seeds with assortative sexual selection and directional selection for bimodal seeds with random sexual selection. These results directly support our hypotheses. Also, when random mating is combined with uniform seeds we again see a single distribution supporting our hypothesis. In this particular case the population is not attracted to a particular seed size as was the case for bimodal seeds but instead performs a random walk with respect to beak size.

The most interesting case is when assortative mating is combined with uniform random seeds. We hypothesized that we would see pseudo-speciation supporting a given number of populations. This was supported by the data we collected. We didn't anticipate the diverse branching (and less frequent) merging seen across the beak/seed range for the 1x case. We observed long term stability in these new populations, remaining distinct for fifty generations or more. In the 10x case we found four stable populations.

7.1 Uniform Seeds

For both cases with 5000 uniform seeds (USAM and USRM) only the individuals at the tails of the distribution survive, see section 6.65 for the USAM case. This is because there is a poor match between the distribution of beak sizes and seed sizes. The initial Gaussian population is very dense around the mean beak size (5.5), and the birds with those beak sizes are dying off. The birds have a fixed seed size range that they can eat and there are a lot of them competing for the same seeds so they will initially "carve out" the seeds available around a seed size of 5.5. Once the birds with a beak size around 5.5 eat all the seeds around a seed size of 5.5 they will begin dying out leaving only the birds at the tails of the original population where the competition for seeds isn't so fierce. Note that USAM and USRM share the same distributions for the initial populations because sexual selection and reproduction have not happened yet. In the 10x case, the population is exploiting all the niches due to the stability of the larger population sizes.

7.2 Bimodal Seeds & Assortative Mating

In the data collected we found speciation. This finding directly supports hypothesis H1.

We reasoned that to get sympatric speciation, we would need some sort of niches that could be exploited differently by individuals with different characteristics and a mechanism to allow the population to split—that is, not everyone breeding with everyone. At the time we were not certain of the exact mechanism that would cause the split but we assumed that it might be related to the limited availability of food/resources. Given that we created both conditions with BSAM, we reasoned that we would get two nicely separated subpopulations that we could call species. Basically, a female from population A could not select the males from population B and vice versa.

7.3 Bimodal Seeds & Random Mating

In the data collected we found directional selection. These results directly support hypothesis H2.

We reasoned that without the sexual selection mechanism to reinforce the isolation of the populations we would get a single species, and because the resources were concentrated on the two modes, that individuals would be centered on one of those modes. Basically, a female could randomly select a male from the other population but in doing so would reduce her own population's advantage. If an imbalance occurred by random chance between the two populations, one population could be driven to extinction.

Following an initial large scale die-off of the population, inviable hybrid offspring are produced starting after the second generation. Inviable offspring are produced because they have a beak size for which there are virtually no available seeds. These offspring do not survive the natural selection process and hence produce no offspring. Compare this result with the case for BSAM where a very limited number of inviable offspring are produced. By mating with males outside their own sub-population, these females are wasting their reproductive resource.

7.4 Uniform Seeds & Assortative Mating

In the data collected we found pseudo-speciation with a variable number of species in the 1x case. This result directly supports hypothesis H3.

We reasoned that sexual selection would reinforce the isolation of the populations but that because there were no static niches to exploit—there were no discrete seed types to stabilize the dynamics—it wouldn't form such nicely discrete species. So, we determined it would produce multiple pseudo-species.

The maximum number of species supported in this configuration is a function of the seed range (9 units) and the range of the female preference (2 units).

The exact reason that most common number of populations for USAM at generation 1000 was three (see section 6.2.11) is not completely clear but it is related the the female seed/mate preference range along with the range of seeds available. Here the range for the female mate preference and seed preference is the same.

The larger population sizes for the 10x case provided the stability needed to support a constant number of species. In particular, these populations are able to avoid extinction due to a sex ratio imbalance.

It is the combination of natural selection and sexual selection which leads to divergence. Natural selection causes the initial die-off in the center, increasing the variance and essentially forming two new populations, and sexual selection keeps them apart.

7.5 Uniform Seeds & Random Mating

In the data collected we found (at most) a single population. This result directly supports hypothesis H4.

We reasoned that the random mating would (as with BSRM) limit us to a single population but that it wouldn't be found at a particular beak size since no modes existed. We also speculated that the beak size distribution might be broader than in USRM than in BSRM because in USRM there were seeds spread out and available everywhere and concentrated nowhere.

Without assortative mating, branching does not occur.

7.6 Evolutionary Biology

Our findings are congruent with earlier empirical studies that indicated an important role of female choice (Bleay and Sinervo, 2007; Boake, 2000; Boughman, 2001; Seehausen and van Alphen, 1999). It is also noteworthy that sexual selection using beak size has been implicated in other finches, too (Slabbekoorn and Smith, 2000).

While confirming a prediction was excellent proof for the utility of the modeling approach, our findings using uniform seeds and assortative mating were completely new and unpredicted. Here we find clear signatures of divergence (as bifurcations in the plots), but no clear patterns of long-term speciation in the 1x case. This underscores even more the role of female mate choice for actual speciation.

The present model of sympatric speciation is capable of creating divergence in a situation where speciation would be predicted by theory: when the food resource came in two discrete size packages, the birds showed adaptation to these sizes and evolved into two groups. This divergence was reinforced by female choice—females preferred males with similar beaks.

7.7 Artificial Life

We found support for speciation but we did not introduce physical barriers into our environment to do so like Yaeger (1994). In fact the only spatial aspect of the work in this dissertation is the location of each individual seed which was used to limit the rate at which the seeds were consumed.

We also found that agent based models are well suited to ecological simulations (Carnahan, 1997). Although we did not work with the equation based approach in our work—a direct comparison is not possible (nor is it in the scope of this work)—the agent-based approach was able to satisfy our simulation requirements.

Similar to Gras et al. (2009), we demonstrated the emergence of species as a result of behavior. In their work they evolved the behavior using a fuzzy cognitive map. Although their simulation also generated a lot of data they could not provide a clear visual representation of the speculation process due to the inherent complexity of their genotype/phenotype. In addition, they explicitly encoded the concept of a species using a cluster model based on a genomic distance metric. In our work, the assortative mating rule implicitly creates clusters of individuals.

Our environment was able to support multiple species using a single phenotypic trait. By using a single phenotypic trait, we were able to avoid the complexity associated with multiple traits (Kampis and Gulyas, 2004).

We have made progress toward the goal of open-ended evolution. Our demonstration of niche selection in relation to mate selection in part satisfies the future work proposed by Chaumont et al. (2007). We also found that our framework "is particularly well suited to designing experiments that would be impossible, impractical, or unethical to perform on biological organisms and communities" (Chaumont et al., 2007).

7.8 Evolutionary Computation

We also found that an interdependent fitness landscape leads to sympatric speciation (Ebner et al., 2010). We use an implicit fitness function—our fitness is based solely on reproductive success of the individuals. The connection to their results is clear, the individuals in our environment are using the resources (seeds) within each individual's range and thereby affecting the fitness of the other individuals.

In some cases, this competition can lead to death due to starvation. This competition for one type of resource (food) then affects the competition for another type of resource (mating).

7.9 Small Populations

A population containing a small number of females is more likely to go extinct than a population containing a small number of males because males can mate with multiple females while females can only mate with a single male in any given year.

In the directional selection case (BSRM) what we see is possibly a result of small population size but the result is still valid. Small population size is a factor that has been largely unexplored by current research. The finch populations on which we are basing our simulations have small population sizes so there is a biological basis for this discussion. The research performed in this dissertation may have an impact on the biologists studying small population sizes in general. The possibility of extinction is always a concern with small population sizes and is of particular importance in the study of speciation.

More investigation is needed but larger population sizes may affect the conclusions drawn for BSRM. If larger population sizes are tested—at least two orders of magnitude larger than our smallest case—we might expect to see two populations supported. We saw some support for this in our 10x case. As the population size increases, the probability for one population to randomly go extinct should decrease. There are major two sources of randomness, random mate selection and random gender. If the sex ratio is not balanced then there could be fewer females than males which could cause extinction. Fewer females is a problem because females can only mate once per year while males can mate up to four times.

It is possible that two BSRM species could be supported with small population sizes. In the present model, recombination is simulated as a blending of two phenotypic traits to determine beak size. It is possible that, with a discrete allele set, we might see two interbreeding populations lasting for an indefinite time period. The challenge is to come up with a discrete allele set that could support the expected outcome.

7.10 Complete Extinction Events

In order to survive in our environment, a population must be able to bootstrap from a small initial population size and remain stable for many generations.

In both cases that use random selection, complete extinction due to behavior is not possible because females can select from all males. It is possible that the initial population could be all male or female but this is an unlikely event.

Bimodal seeds and assortative mating resulted in the lowest number of complete extinctions (Table 6.2). Complete extinction in this configuration is possible but apparently highly unlikely–implying that this configuration is stable. One of the two branches would go extinct but not both.

7.11 False Starts

False starts due to initial conditions (Table 6.5) are the roughly the same for each column because they depend only on the initial population. Sexual selection is not a factor because it has not taken place yet when initial populations are determined.

False starts can be caused by a small initial population size. Comparing initial population sizes (Table 6.7) with the number of false starts due to initial conditions (Table 6.5) it appears that smaller initial population sizes lead to more false starts. It appears that there is a threshold for the initial population size over which false starts are not likely.

False starts due to random mating behavior can not occur because the female will always select the last remaining male to mate with. There are no false starts to report for the bimodal seeds and assortative mating case because there were no complete extinctions (see Table 6.2.

False starts can be caused by a combination of small initial population size (due to the uniform seed distribution) and the assortative mating behavior (Table 6.6). This can happen when all the females are in one sub-population and the males are in the other at the start of sexual selection. If there is enough separation of the populations with respect to beak size, then the females will not select males from the other sub-population because of their small preference range due to assortative mating. In this case, females will not select males from the other sub-population even if they face extinction.

CHAPTER 8

Conclusions

In this dissertation we have addressed interesting questions related to mate selection in our ecological simulation and provided significant contributions with our work.

The first question regarding the ability of the population to track resources was addressed. We found that our simulated bird populations evolved specialized beaks for the food resources available.

The second question regarding the role of female mate preferences was addressed. We found that sexual selection based on assortative mating was necessary for divergence. This effect may be due to the small population sizes that we used, but more investigation is necessary.

I believe that we have captured the essence of the finch studies on the Galapagos islands. By focusing on one particular phenotypic trait we have demonstrated how a highly variable beak size along with the process of natural selection and sexual selection can lead to speciation.

We believe that this dissertation is the beginning of a multi-year research endeavor. In particular we are interested in understanding the role of behavior with respect to sympatric speciation. I believe that what we learned in this work will allow us to effectively explore different complex forms of behavior and in particular the evolution of learning.

I believe we have made a number of significant contributions which are listed below followed by a discussion of each individual contribution.

1. Four hypotheses, in which we reasoned using first principles, where we expected to find speciation for the combination of two different sexual selection methods and two

different environmental conditions.

- **H1** For random bimodal seeds and assortative sexual selection we expect to find speciation.
- **H2** For random bimodal seeds and random sexual selection we expect to find directional selection (no speciation).
- **H3** For random uniform seeds and assortative sexual selection we expect to find pseudo-speciation.
- **H4** For random uniform seeds and random sexual selection we do not expect to find speciation.

2. Demonstration of sympatric speciation using a minimal set of biologically realistic constraints.
3. Phenophylogenetic tree for visualizing the phenotypic character of each individual in a phylogenetic tree.
4. Repeated extreme natural selection event in which the food resource is gradually exhausted due to the feeding behavior of the individuals.
5. Individual-based simulation stabilized with respect to boom-bust cycles.
6. Object-oriented simulation framework for ecological systems.

We found experimental support for all four hypotheses. In the data collected we found speciation for bimodal seeds with assortative sexual selection and directional selection for bimodal seeds with random sexual selection. These results directly support hypotheses H1 and H2. When assortative mating is combined with uniform random seeds we found diverse branching and (less frequent) merging supporting hypotheses H3. When random mating is combined with uniform seeds we found a single distribution supporting hypothesis H4.

In this work, we limited the overall number of constraints in our system and focused on two key parameters: mate preference and environmental conditions. In contrast, most biological studies include many of the low-level details of an organism. In artificial life, researchers typically develop an elaborate model of the individual in their environment. We feel that our focused approach on the details required to support sympatric speciation is an important distinction.

We felt that visualization of the speciation process was an import factor in the success of our research. Of the many methods we tried and tested, our phenophylognentic tree was the best way to help us form a good mental model of the process. Using this approach, we can see both the distribution of the beak sizes and mating behavior, in particular hybridization, in one plot.

Another important aspect of our work is the modeling of the extended dry season found in the Galapagos islands. In our simulation we captured the day-to-day dynamics of birds feeding on a limited supply of seeds. I believe that this unique aspect of our work was a key factor in the rapid evolution of our populations because of the large selection pressure it created.

Considerable effort was put into the stabilization of the evolutionary dynamics. We employed a number of methods to avoid the boom and bust cycle leading to complete extinction. Although increased extinction is a known consequence of small population size, we wanted enough stability to be able to draw conclusions about speciation. In the future, we would like to automate this process by incorporating parameters such as clutch size in the genome itself.

The work in this dissertation is a result of an interdisciplinary collaboration between biology and computer science. One of the important contributions from computer science in this work is the extensive set of tools available for the modeling of objects. In particular, the well-developed object-oriented techniques for software development are a nice fit for our ecological simulation needs.

CHAPTER 9

Future Work

This work can be extended in the follow ways:

1. Mining the existing data for more knowledge. We made a significant a contribution in the qualitative analysis of the data with our phenophylogenetic graphs. We would like to extend this work to a quantitative analysis of the phenomena we observed. One possibility is the automatic identification of different species. Manually identifying the different species is a tedious process especially when the populations are not well defined. With this new capability we could gather statistics for each population such as size and sex ratio which may be useful in predicting extinctions.

2. Validation of the data. We would like to work with Peter and Rosemary Grant to validate our simulations. Although we have used key principles from biology in the design of our simulation, we are interested in validating our results with actual finch data. Additionally, we feel that observing the birds in their natural environment would benefit us greatly. A field study could provide us with valuable knowledge which would improve our research and lead to better interaction with biologists.

3. Collecting more results. A biologist might expect that two populations could be supported in the BSRM case if the population size is large enough. The expectation is that although a large number of offspring die during natural selection a large enough population could stabilize the dynamics. After increasing the seed count by ten times, we still found a single species supported at generation 1000 which contradicts this view. By running our simulations we could help answer this question.

Optimization is an important consideration when increasing the seed count. The critical path for our current architecture is the process used to model the spatial foraging behavior of the individuals. Improving the efficiency of this algorithm could greatly reduce the simulation run time.

4. Minor modifications to the framework. New genetic representations could be explored which may allow multiple species to exist with small population sizes for the BSRM case. In the current framework we use a floating point number to represent the beak size but we anticipate using alternative representations with a discrete set of alleles.

   We are also interested in exploring the co-evolution of beak and seed sizes. In our current simulations, the seed sizes are static and the initial distributions known in advance. On the Galapagos islands, the plants which produce the seeds that we model are under the same selective pressure as the birds. We feel that the co-adaptation of birds and seeds will lead to new insights.

   In the current implementation we used a greedy feeding behavior for each individual. Basically each individual consumes an entire seed independent of their energy level. In an alternate approach, the individual only consumes the energy it needs leaving part of the seed behind. We are interested in how this change affects the population size.

   Nurturing is another concept we would like to explore. Small changes to our framework would allow us to study the effects of parental investment on the population.

We believe that the knowledge we have gained is broadly applicable to other areas of research.

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