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EVOLVING SPECIALIZATION IN AN AGENT-BASED
MODEL WITHOUT TASK-SWITCHING COSTS

by

SHANE ROBERT MEYER

A DISSERTATION

Presented to the Faculty of the Graduate Schools at
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ABSTRACT

This work examines the possibility of evolving the phenotypic specialization associated with division of labor in an agent-based model without task-switching costs. The model examines two groups competing for vital resources, where members of one group are capable of sharing resources with other agents in their group. Agents attempt to collect resources which allow them to reproduce, with more resources leading to a greater number of offspring by asexual reproduction. Four variants of the model are examined, with combinations of one or two resources and the presence of a foraging risk. The presence of the foraging risk can lead to agents in the sharing group specializing in each trait but, by looking at the fraction of foragers per generation, this event appears to be a transient state. Division of labor is quantified by calculating the normalized mutual entropy, and is shown to be higher when a population contains agents which specialize on different tasks.

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1. INTRODUCTION

Biological evolution is often referred to as gradual change in gene frequencies over long periods of time. Natural selection can be summed up succinctly as heritable variation in fitness, due to factors such as predation and competition for resources. A population may have some members removed due to selection, and the survivors may reproduce, with possible mutations in genes which may allow adaptation to the environment. Mutations which are beneficial to the organisms will become more common in future generations. While these statements are agreed on by anyone studying the topic of evolution, the details of how some evolutionary changes occur is a matter of considerable debate.

1.1. ALTRUISM

One of the biggest questions within the topic of evolution is how altruistic traits can evolve and become stable (Kerr & Godfrey-Smith 2002, Frank 2013). The primary issue with altruism is due to the idea that all selection occurs at the individual level, and therefore only traits which allow a gene to make more copies of itself should be favored over many generations. The general argument is that if a gene exists that causes an organism to sacrifice its own ability to reproduce, or to otherwise reduce its probability to produce offspring, then that gene should disappear because organisms carrying the gene would be outcompeted by conspecifics. Before addressing the question of how altruism can evolve, it is necessary to consider where selection occurs.

1.2. LEVELS OF SELECTION

It is often said that selection acts on the phenotype, i.e. selection acts on the traits an individual has which can interact with the environment. This selection is sometimes referred to as being selection on genes when individual genes, or combinations of genes, are responsible for the traits in the phenotype. This is perhaps not the only way that selection can act on genes. It is also possible that there can be selection within the genotype, with genes which help to stabilize the rest of the genome and prevent

mutations also being selected (Doolittle & Sapienza 1980), but it is unknown if this type of selection occurs.

While Okasha (2006) uses “individual selection” in a more general sense to mean selection on any single unit (as opposed to a collective of units), this work will define individual selection as selection on the phenotype of an organism. This phenotype consists of traits which may be a result of specific genes, but can also be a result of developmental processes (Sears 2014). Even though selection ultimately results in passing on (or not passing on) the genes of the organism, it is the phenotype which is selected for (or against).

1.2.1. Group Selection. Since a combination of genes which produce a trait can be acted on as a whole, then it is reasonable to think that combinations of individuals with different phenotypes could produce different group traits and these could also be acted upon. This idea is referred to as group selection (Smith 1964, Wilson 1975, Okasha 2006, Gardner & Grafen 2009). Group selection requires that individuals which are in a collective (multicellular organisms, insect colonies) interact to produce a group phenotype, and that this group phenotype differs from another group’s phenotype, thus leading to selection at the level of the group. These group phenotypes would also depend on the traits of the individuals within the group, and the idea is that a group with more cooperative individuals would have an advantage over a group with purely selfish individuals. Essentially, because an altruistic trait lowers the fitness of the altruistic individual, altruistic traits can only be retained due to some type of selection acting on the group.

A major problem with group selection, as it is typically described, is that it does not address a pathway for altruistic traits to survive. If an individual with an altruistic gene sacrifices its fitness for the good of the group, then it reduces the probability of the next generation having this altruistic gene.

1.2.2. Kin Selection. This problem is partially solved by kin selection, where the altruistic gene can still propagate among a group if some members sacrifice their fitness in order to provide a benefit to their kin, who might share the altruistic gene. The condition for kin selection is given by Hamilton’s rule, $c < rb$, where r is the genetic

relatedness (defined as the proportion of shared genes by common descent) between the individual engaging in the altruistic behavior and the recipient of said behavior, b is the benefit that the recipient receives, and c is the cost to the engaging individual. As long as this inequality holds, then altruistic genes can be maintained. Kin selection is a simple concept, and easily understood. It is considered the correct explanation for some altruistic behaviors in nature (Browning et al. 2012, Suegene et al. 2018, Yamauchi et al. 2018), but it does not explain situations where an organism decreases their reproductive fitness for entities which are largely unrelated. Group selection then becomes a more likely candidate, but this may still be dependent on the type of behavior, e.g. cooperation.

When multiple groups of organisms occupy an area, there can be competition between groups, allowing for some types of cooperation within one group to confer an advantage allowing the entire group to thrive (Gavrilets & Fortunato 2014, Shaffer et al. 2016). Naturally, cooperation is vulnerable to cheaters (Czárán & Hoekstra 2009, Boza & Számadó 2010, Celiker & Gore 2013, Queller & Strassmann 2013), individuals who receive the benefits of cooperative behavior without engaging in the behavior themselves, and it may be necessary that some systems rely on conflict suppression (Michod et al. 2003, Rainey & Rainey 2003) to prevent cheaters from overwhelming the system. Group selection has also been invoked to explain some social behaviors that occur in nature, where organisms which are not direct kin, but are still in the same species, form colonies together, e.g. ants (Shaffer et al. 2016) and spiders (Pruitt & Goodnight 2014). However, it may be that these collectives are not stable formations, as they appear to have a higher rate of extinction than similar species which are not social, at least among spiders (Pruitt & Avilés 2017). Of course, there are some social behaviors which are assumed to be both stable and extremely advantageous, the most notable of which is division of labor.

1.3. DIVISION OF LABOR

Division of labor is present across all levels of biological organization, from eukaryotic cells, to eusocial insects, and human societies. The extent to which division of labor is present in various forms of life indicate that it may be extremely easy to evolve, and advantageous to the organisms engaging in division of labor. Division of labor ranges from an extreme case of altruism to a changing process of task allocation. The

altruistic type of division of labor occurs in honeybees, termites, wasps, and all species of ants, where a non-reproductive worker caste serves to take care of the offspring of their queen. At the other extreme, organisms can take up different tasks depending on context, but still distribute work so that all of the needs of the group are met. In some cases task allocation may be dependent on the age of the organism, a property known as age (or temporal) polyethism. Of particular interest is how tasks are allocated at a given time.

The ants *Leptothorax unifasciatus* and *Pogonomyrmex californicus*, and the bumblebee *Bombus impatiens* are all known to have a spatial component of task allocation (Sendova-Franks & Franks 1995, Holbrook et al. 2013, Jandt & Dornhaus 2009); an individual's location in the colony/nest indicates the types of tasks the individual engages in. Individuals which are closer to brood engage in brood care, or individuals at the edge of the nest may engage in defense or foraging behavior. *Bombus impatiens* is also influenced by age, because as a bumblebee ages they tend to travel toward the edges and outside the nest (Jandt & Dornhaus 2009), with brood located at the center of the nest being taken care of by the youngest bumblebees, and foraging behavior engaged in by the oldest.

The phenotype of an organism may also determine the tasks it engages in. This is the case in honeybees (Johnson 2010), halictine bees (Jeanson et al. 2005), and eusocial wasps (Torres et al. 2011). Some ants may actually have a predisposition not to work, as was found in *Temnothorax rugatulus* (Charbonneau & Dornhaus 2015). It is also possible for some types of behavioral differences to depend on age, as it is known to affect the expression of the *Foraging* gene in the ant *Cardiocondyla obscurior* (Oettler et al. 2015). Gordon (2016) suggests that task allocation due to behavioral differences is the only true division of labor; though such a statement ignores that spontaneous task allocation (Simpson 2012) could have arisen as an answer to non-constant needs, e.g. colony defense, which is obviously an important and risky task (Breed et al. 1990).

Division of labor is most well studied in insects, but is obviously present in other types of organisms. Kim et al. (2015) showed that a strain of *Pseudomonas fluorescens* could evolve division of labor in a matter of days via a single mutation, indicating that at the bacterial level the evolution of division of labor may be both simple and repeatable. The differentiation in multicellular organisms between germ and soma is another well-

known example, but division of labor is also present in the behavior of slime molds, most commonly *Dictyostelium discoideum* (Bonner 1998, Bahar 2018), where individual amoebae aggregate to produce offspring. Some of the amoebae that were acting in their own interest prior to aggregation will form the stalk of a fruiting body, and not reproduce.

1.4. MODELS OF DIVISION OF LABOR

There are two general categories of models in the subject of division of labor: mechanistic and evolutionary (Duarte et al. 2011, Beshers & Fewell 2001), each with a different overall goal.

1.4.1. Mechanistic Models. Mechanistic models focus on describing a particular species or type of division of labor and the possible cues that cause task allocation. Models of this type include response threshold, foraging-for-work, and interaction models. They focus on describing division of labor as a property which emerges due to the behavior of the individuals and generally assume that division of labor exists in the system already, with the goal of providing hypotheses for the mechanisms behind it.

Bonabeau et al. (1996) studied what is known as the fixed response threshold model, focused on describing the behavior of the ant *Pheidole pubiventris*. The fixed threshold model assumes that all organisms vary in their sensitivity to some stimulus in the environment, and when the level of stimulus increases to that organism's response threshold, then the organism engages in the task, lowering the stimulus level, until the stimulus drops below the threshold. Theraulaz et al. (1998) modified this model by allowing an individual's response threshold to change over time, such that the more often the individual engaged in the task, the lower its response threshold would be for that task at a later time. Richardson et al. (2011) added a physical space to the fixed threshold model, and this had the effect of producing individuals with higher thresholds which would become active when the individuals with lower response thresholds were not as close to the source of the stimulus.

Foraging-for-work models are similar to response threshold models in that they describe how task allocation can change in response to changing needs, and as a function

of worker age (Tofts & Franks 1992), though they are criticized for being unable to show any inactive workers (Beshers & Fewell 2001).

Interaction models assume that social interactions are the primary cause of division of labor, that interacting agents can transfer some information about the work they have performed, or the work that is needed, and that this is how new workers are recruited (Duarte et al. 2011).

1.4.2. Evolutionary Models. Evolutionary models seek to understand the conditions necessary for division of labor to evolve from a general standpoint, and do not necessarily need to model specific systems.

Ispolatov et al. (2012) modeled the aggregation and differentiation of single cells in order to describe the transition to multicellularity. This model allowed cells to produce metabolites, send chemical signals, and exchange metabolites, with costs that cells tried to minimize. This produced cells which could specialize in a single metabolite, receiving the other from neighboring cells, and that this was a desirable state because the fitness of organisms was higher when they had access to both metabolites. Gavrilets (2010) did something similar, but assumed that cells formed colonies which could differentiate into germ and soma via plasticity. A noteworthy feature of this model is that cheaters were driven out because when they formed their own colonies they were at a disadvantage compared to colonies without cheaters.

From a more abstract perspective, Goldsby et al. (2012) demonstrated that task-switching costs in an agent-based model in Avida could lead to division of labor if agents were allowed to exchange information. Agents in the Avida system are “digital organisms” which compete for processing time and resources by performing logical functions, with more complex functions rewarding a higher amount of resources to the agent performing the function. Because of the exchange of information, agents could work together to perform parts of the function, and send their result to another agent which would perform another part. The design of this model put agents into predetermined colonies, and when the colonies amassed a threshold amount of resources, they produced an offspring colony. Therefore, the colonies which developed division of labor were able to acquire resources more quickly, and replicate more frequently, than colonies without division of labor.

Goldsby et al. (2014) considered a similar system, also in Avida, focused on analyzing the result of conflicting pressures between individual and group levels. They found that not only could sufficient between-group pressures lead to within-group cooperation, but that successful agents were ones that produced more phenotypic diversity. Continuing with models in Avida, Pierce (2012) showed that a model with aging and risky tasks could produce age polyethism, where older agents who had already had the opportunity to reproduce engaged in the more dangerous tasks, so that younger agents would not be at risk before reproduction.

2. MODELS AND ANALYTICAL METHODS

Determining minimal requirements for evolving division of labor is a non-trivial task. Every model of division of labor to date has some form of task-switching cost, either explicit or implicit. Incorporating any form of learning, or plasticity, in a model is an example of an explicit cost, where an organism is more efficient at engaging in one task exclusively. Meanwhile, implicit costs are present when organisms have to travel some distance to engage in a new task, and therefore a physical space will inherently always have implicit task-switching costs. It is known that these kinds of task-switching costs can lead to division of labor (Gavrilets 2010, Goldsby et al 2012). What is not known is if these costs are required. In order to explore a scenario without task-switching costs of any kind, the models described here contain none of the influences that a physical space could have on the system.

Due to the frequent occurrence of division of labor across biological life, it is desirable to consider a system which does not require complex organisms. If constraints on the system are truly minimal, they should be able to affect single celled organisms as well as more complex lifeforms. To that end, the agents in the models described here can be thought of as simple bacteria floating in a jar of nutrients. Another potential question that this work may address is the competitive advantage that specialization and division of labor could endow. For this purpose these models contain two groups of agents in this metaphorical jar, which differ in one detail: the ability to share resources.

2.1. BASIC MODEL

A simulation begins with two groups, each containing five agents, and 10 units of resources. Agents in both groups have two continuous traits which are uniformly randomly distributed on the interval $[0, 1]$. These traits function as sensitivity to stimuli, such as resources or other agents in the individual's group. Furthermore, an agent's trait values affect which task an agent engages in. Each generation consists of a number of turns, and the number of turns per generation is a parameter which is varied. The number of turns is representative of an average lifespan of organisms, as the more turns there are, the longer the agent has to collect resources. Every agent in the population is selected

once each turn to engage in a task with some probability, which depends on both the agent's trait values and the level of stimulus (amount of resources or agents) in the environment. A simple method is to make agents attempt to forage with probability

$$p_f = \frac{\theta_f(R + 1)}{\theta_f(R + 1) + \theta_s(N - 1)} \quad (1)$$

where R is the amount of resources available, $N - 1$ is the number of other agents in the selected agent's group, and θ_f , θ_s refer to the selected agent's foraging and social trait values, respectively. The factor of $R + 1$ was chosen to allow for an agent with a high foraging trait value to attempt to forage even when there are no resources. When an agent forages, it acquires one unit of resource from the environment and R decreases by one. If an agent does not forage, it will socialize with probability θ_s such that

$$P(\text{socialize}|\text{not forage}) = \theta_s \quad (2)$$

where this extra probability prevents agents with low social traits from socializing when there are no resources available. With this conditional probability specified, the total probability to socialize can be written as

$$p_s = \frac{\theta_s^2(N - 1)}{\theta_f(R + 1) + \theta_s(N - 1)}. \quad (3)$$

When an agent socializes, if it is part of the group that is allowed to share resources, the agent randomly selects another agent in its group and they split evenly whatever resources they have acquired at that point. This kind of direct resource sharing does occur in ants via trophallaxis (Richard & Errard 2009). An agent is allowed to do nothing, in the event it does not socialize or forage. The total probability to do nothing can be written

$$p_d = \frac{(1 - \theta_s)\theta_s(N - 1)}{\theta_f(R + 1) + \theta_s(N - 1)}. \quad (4)$$

After all agents have been chosen once in a turn, they repeat the process again in the next turn.

When all turns have been completed, agents have the opportunity to reproduce, marking the end of the generation. Agents which have no resources are removed from the population, while agents with resources reproduce asexually, with a probability which depends on the amount of resource $n.d$ they collected in that generation. The number of offspring that an agent has is $O = n+1$, with a probability $0.d$ to have an additional offspring. For example, suppose an agent has collected 2.5 units of resource through some combination of foraging and sharing. Then the agent has at least 3 offspring, with probability of 0.5 to have a 4th offspring. An agent which successfully reproduces is removed from the population. Note the special case when an agent collects less than 1 unit of resource. If the agent does not reproduce, but $d > 0$, then the agent survives to the next generation.

Offspring are given trait values which are each uniformly randomly distributed within $\pm\mu$ of the parent's trait values. The value μ is referred to as the mutability, and is simply the maximum amount an offspring can vary from the parent. If an offspring agent is given a trait value which is less than zero, or greater than one, the agent is removed from the population.

After all agents have attempted to reproduce, the new generation begins with the offspring and non-reproductive survivors of the previous generation. At the beginning of every turn (including the first one), the amount of resources in the environment increase as a logistic equation given by

$$\frac{\Delta R}{\Delta t} = 2R\left(1 - \frac{R}{R_{max}}\right) \quad (5)$$

where $R_{max} = 100$. As R_{max} determines the maximum amount of resources in the environment, it puts a soft limit on the number of agents in each generation. Setting this

at 100 allowed populations to be large enough to see significant trends in distribution of trait values, yet small enough as to keep computational time at a reasonable level.

2.2. MODIFICATIONS

There are two additions to the model that are considered in this work. The first is a risk of foraging, which is present as a probability of an agent dying and being removed from the population when attempting to forage. This risk was motivated by the idea of an organism leaving the safety of its nest to find food and being eaten by a predator. Another interpretation of this risk, one which is more consistent with the idea of simple organisms in a jar, is that a small amount of contaminated food source is present. The probability that an agent is removed from the population when foraging must be small if the population is to survive at all. Multiple values were tested and it was seen that if this probability was 0.2 or higher, that populations would rarely survive more than 10 generations. Therefore, values that were used were kept under 0.1 for the risk to have an effect without eliminating population of simulated organisms.

The other modification considered adds a second resource, and a corresponding additional foraging trait. In this version, one resource is vital for survival, while the second resource allows for offspring. Agents have three traits: one trait controls foraging for the survival resource, one controls foraging for the reproductive resource, and the third is the social trait. This version of the model will also be considered in situations with or without a foraging risk, making for a total of 4 versions presented in this work.

2.3. IDENTIFIERS OF DIVISION OF LABOR

It is important to have a clear way of identifying when division of labor occurs. Three different concepts of division of labor will be considered in this work: normalized mutual entropy, distribution in trait space, and fraction of foragers.

2.3.1. Normalized Mutual Entropy. The normalized mutual entropy is the standard measure of division of labor. Also used in ecology to measure biodiversity (Gorelick et al. 2004, Gorelick 2006), mutual entropy, when applied to division of labor, gives information about which individuals engage in which tasks. Given a matrix P

where rows are individuals and columns are tasks, an element p_{ij} gives the probability that individual i engages in task j . This matrix can be constructed from real data, where the probabilities are instead observed frequencies, or the percent of time that organisms engage in tasks (Goldsby et al. 2012). In this work, these matrices are constructed from the previously mentioned probabilities: p_f , p_s , and p_d . The mutual entropy I is denoted as

$$I = \sum_{i,j} p_{ij} \ln\left(\frac{p_{ij}}{p_i p_j}\right) \quad (6)$$

where p_i and p_j are the marginal probabilities. Because the matrix P is a probability matrix, the marginal probabilities p_i and p_j are the sums across the columns and rows of P , respectively, and $\sum p_i = \sum p_j = 1$. For the models in this work, each $p_i = \frac{1}{N}$, while p_j will vary depending on the trait distribution. The normalized mutual entropy is then defined as $D = \frac{I}{H}$, where H is Boltzmann's marginal entropy given by

$$H = - \sum_i p_i \ln p_i \quad (7)$$

where the p_i are the same as in the equation for I . The quantity D will be maximized when every individual engages in a single task. It is clear that the models in this dissertation will typically have more individuals than tasks, and it will be unlikely that each individual always engages in a single task, i.e. that every agent's probability to engage in a specific task is equal to one. Because of this, the quantity D will never be equal to one in these models.

2.3.2. Trait Space Distribution. In this dissertation, all of the agents in the models have quantifiable traits, which can easily be placed on a scatter plot. Division of labor should occur when there are two distinct groups on the scatter plot: some with high foraging & low social trait values, and some with high social & low foraging trait values.

This method is based on the idea that phenotypic differences lead to task specialization, especially in highly adapted organisms, e.g. leaf-cutter ants (Wilson 1980). However, variation in traits does not guarantee division of labor will occur.

2.3.3. Fraction of Foragers. The resources in this model are the limiting factor in determining task allocation. It is therefore useful to examine how many agents in the population forage during a generation. This quantity will be determined as the total number of foragers in a generation, divided by both the population size. As there can be more than one turn in a generation, this number may occasionally be larger than one, but never larger than the number of turns per generation. It will be maximized when all agents forage every turn in a generation. This quantity is useful when plotted versus generations for a given run, and can reveal generational variations in task allocation.

3. RESULTS OF SINGLE-RESOURCE MODEL

Before analyzing the various modifications of the model, it is important to see the results of the basic model to be certain which effects are a result of the foraging risk, and which are a result of the presence of an additional resource. Presented here are extinction rates, times to extinction, population vs time and trait distributions for sample runs, and average final populations, for these different cases. Sample runs are shown for the purposes of identifying potential fitness advantages of sharing that might not be detectable in the averaged data, and examining the distributions in trait space which correspond to such advantages.

3.1. SINGLE RESOURCE WITHOUT FORAGING RISK

Simulations are run for 3000 generations, with parameters varied from 1 to 4 turns per generation, and five values of μ on the interval [.01, .09].

3.1.1. Sample Runs for Single-Resource Model. For the case when there is only 1 turn per generation, there is no benefit from the social trait in the sharing group, and both groups evolve to have the same general trait distributions: low social and high foraging values (Figures 3.1 & 3.2). Note that the trait distributions become more diffuse as μ is increased. Looking at the population vs. generation (also referred to as population vs time) plots, it is seen that the population size of the two groups exhibits anti-phase oscillations as is seen in biofilms competing for the same resource (Liu et al., 2017), provided that both groups survive. These anti-phase oscillations persist even at 2 turns per generation, when $\mu = 0.01$ (Figure 3.3). Reasons for this behavior include that the population sizes are limited due to a finite amount of resources at any time, and the two groups have the same distributions in trait space, resulting in no behavioral differences. One group may acquire a majority of the available resource in one generation, and the other group may acquire a majority in the next generation.

The stochastic nature of the model can affect the stability of the two groups, as shown in Figure 3.4, for $\mu = 0.03$ at 2 turns per generation. Here, the population vs. time plots show different behavior on separate runs of the simulation: in one case, both groups

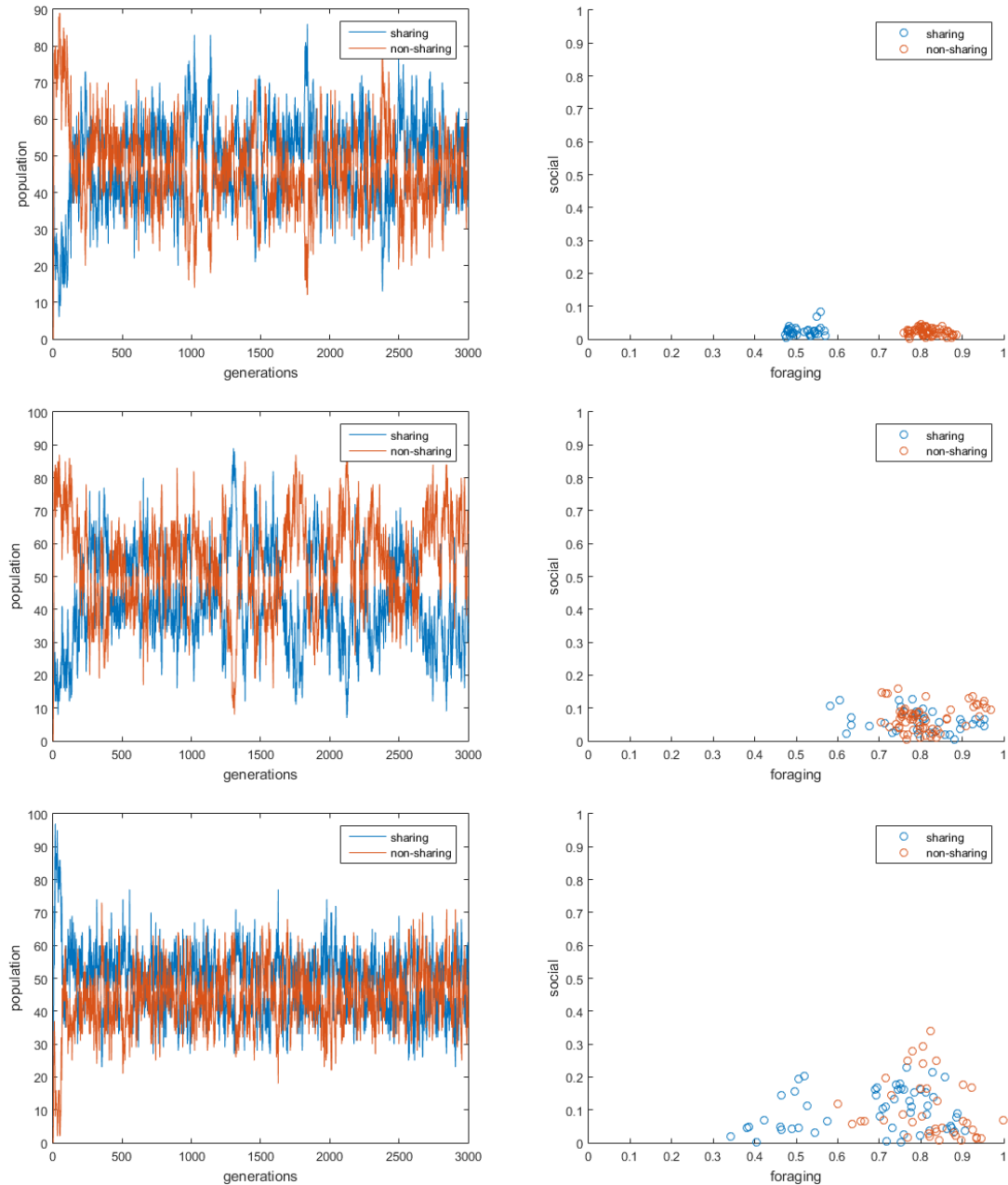


Figure 3.1 Sample runs at 1 turn per generation. Population vs. time (left column) and trait plot (right column). From top to bottom $\mu = 0.01, 0.03,$ and 0.05 . Blue is the sharing group and orange is the non-sharing group.

keep similar population levels, and in the other the non-sharing group holds a large advantage over the sharing group. Examining the trait distributions for these different behaviors demonstrates that the occurrence of high social trait values in the sharing group corresponds to a lower total population size compared to the non-sharing group. But if the sharing group has no members with a high social trait value, then both groups

maintain a comparable size. Interestingly, the social trait did not appear in any runs when $\mu = 0.05, 0.07, \text{ or } 0.09$ (Figure 3.5).

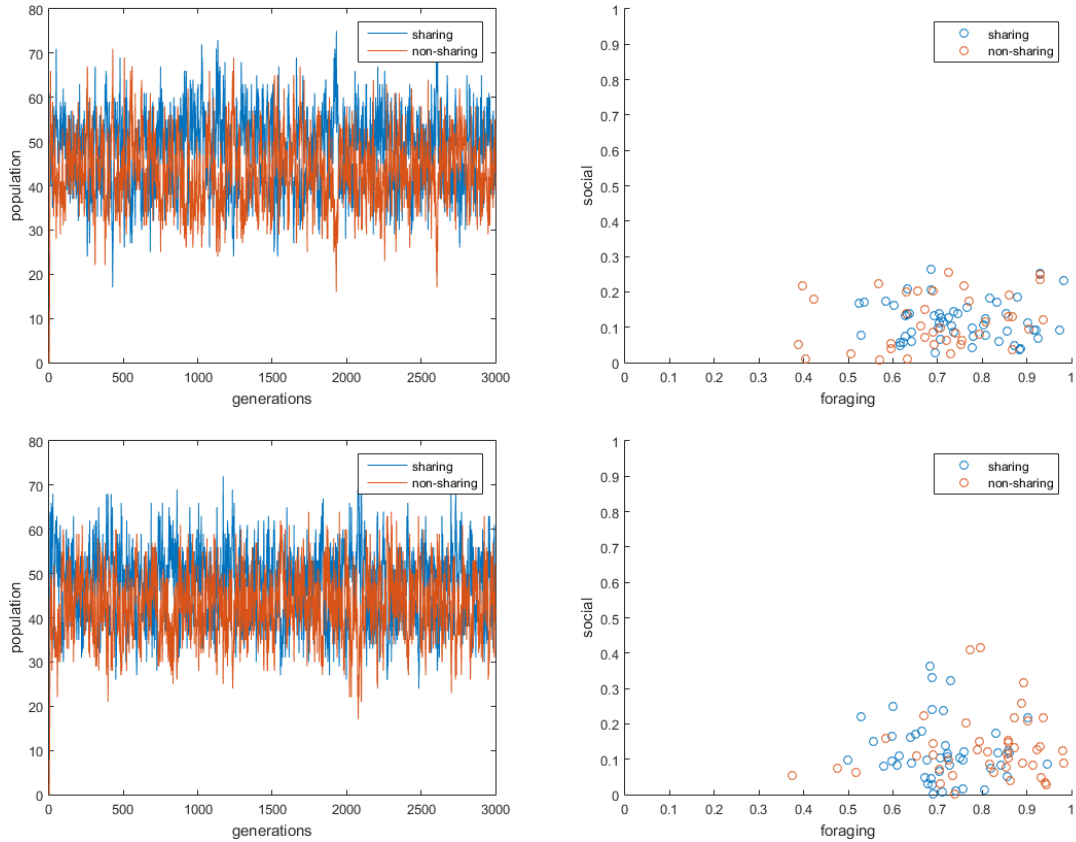


Figure 3.2 Sample runs at 1 turn per generation for $\mu = 0.07$ (top) and 0.09 (bottom).

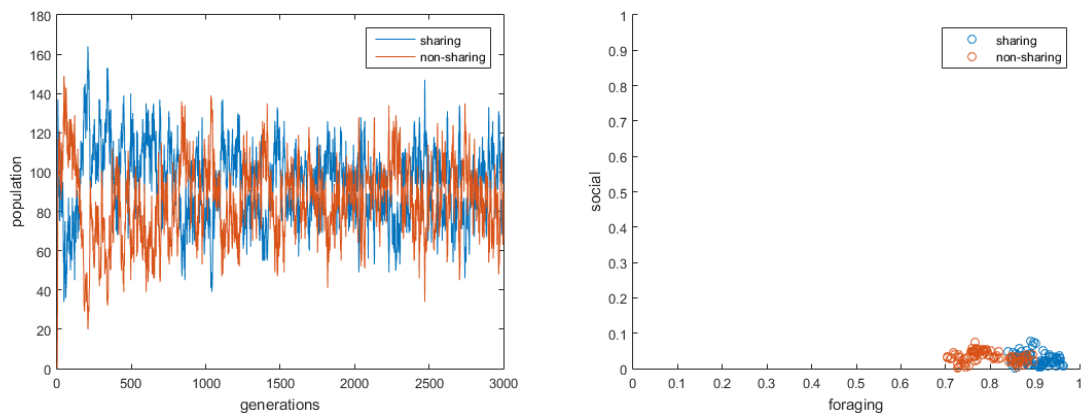


Figure 3.3 Sample run with $\mu = 0.01$, and 2 turns per generation.

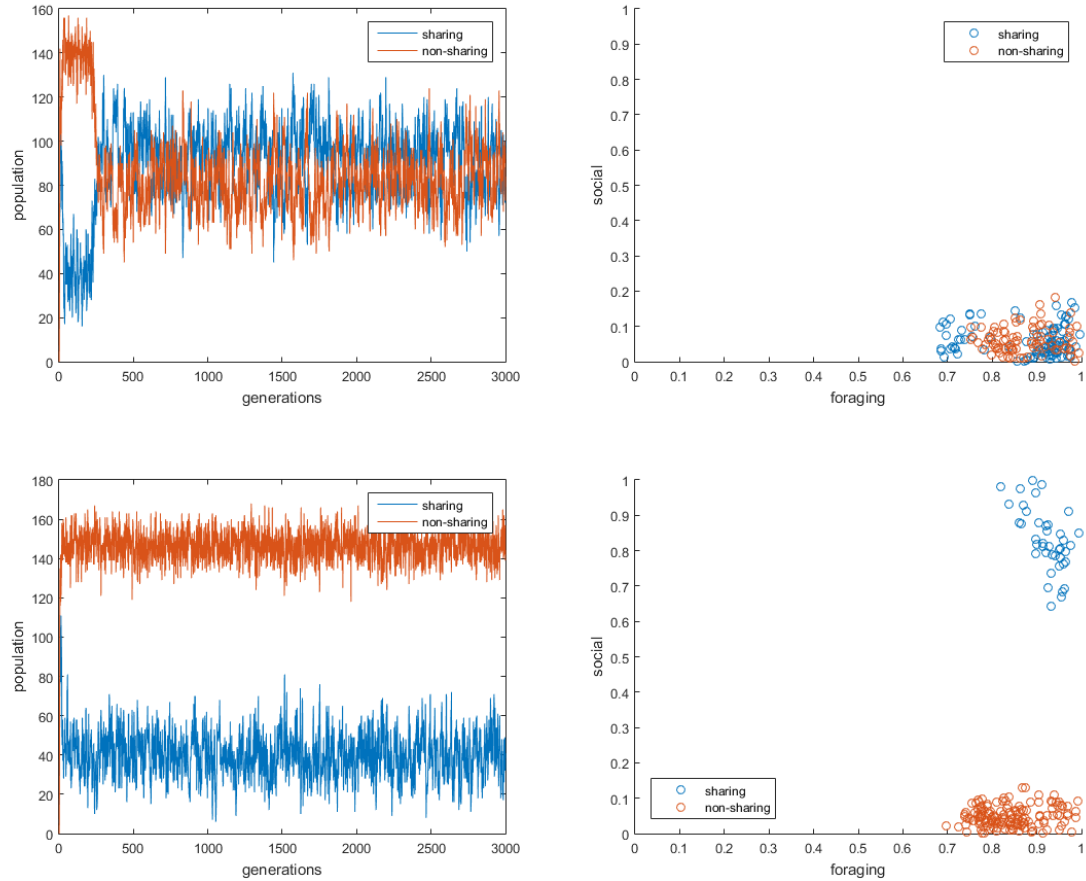


Figure 3.4 The stochastic nature of the model. Parameters for both rows are $\mu = 0.03$, 2 turns per generation.

At 3 turns per generation, that same instability appears to have a wider range of existence, from $\mu = 0.01$ to $\mu = 0.05$ (Figures 3.6-3.8), and can even appear in the same run; as seen in the population vs. time plots in the second row of Figure 3.6 and Figure 3.7. However, at $\mu = 0.01$, the presence of even a small number of agents with low social values in the sharing group (Figure 3.6, top row) appears sufficient to keep population sizes of the two groups at a comparable level. When there are only social foragers, the non-sharing group has a larger size than the sharing group by approximately 100 members (Figures 3.6-3.8). But when $\mu = 0.07$ or 0.09 , the sharing group typically maintains a comparable population size to the non-sharing group, with even a slight advantage (Figure 3.9). The trait distributions in these situations show that the larger mutability parameter allows agents to have trait values in a large portion of the possible space, and this may be connected to the larger population size in the sharing group. The

larger μ value does not benefit the non-sharing group, because a high social trait is always a negative for those agents.

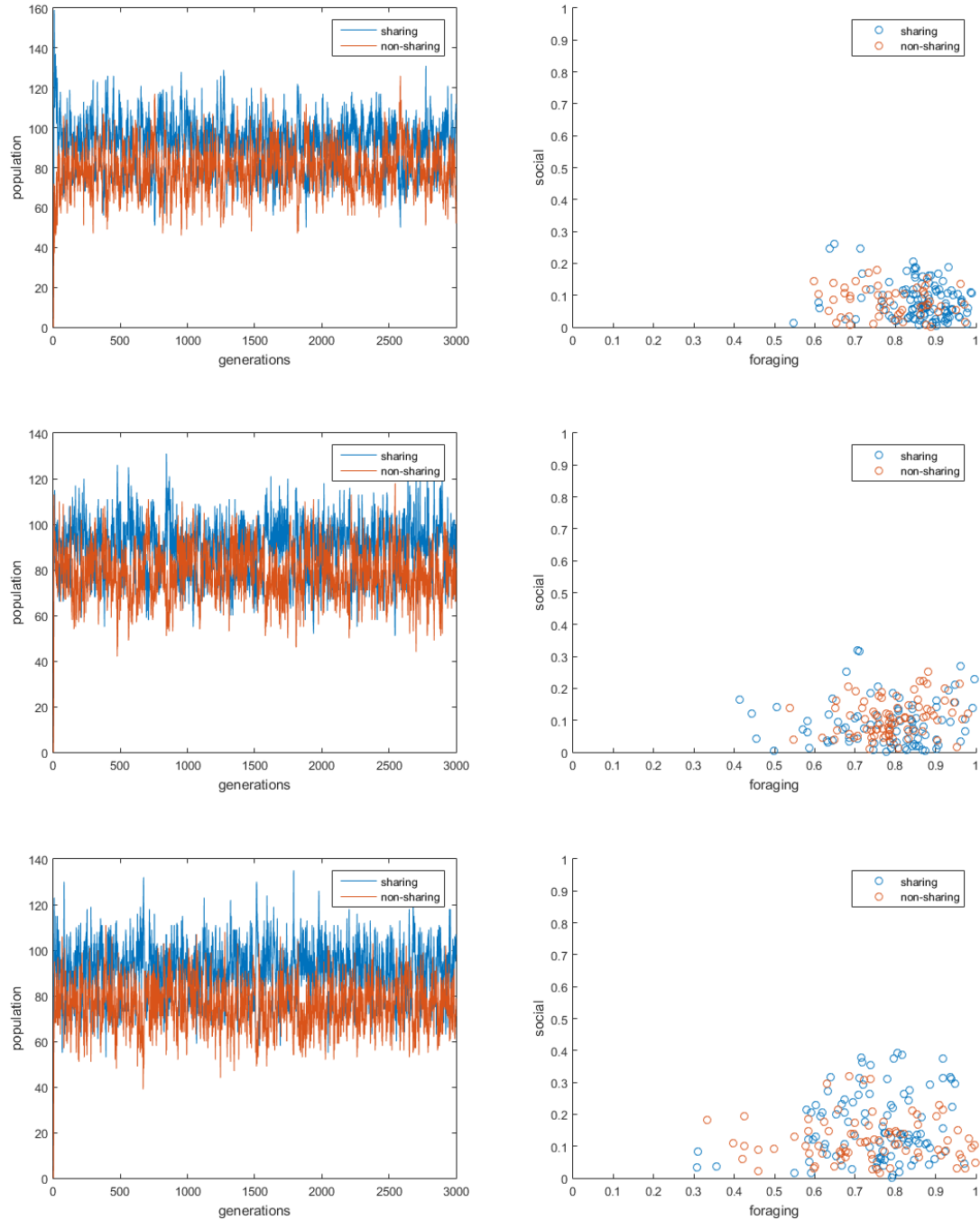


Figure 3.5 Sample runs at 2 turns. From top to bottom, $\mu = 0.05, 0.07, 0.09$.

In the case of 4 turns per generation, the unstable behavior is again present when $\mu = 0.01$, and to a lesser extent when $\mu = 0.03$ (Figures 3.10 & 3.11). For these mutability values, when there are only social foragers (agents with high trait values in both social and foraging traits) in the sharing group, it has a smaller population size than the non-sharing group. However, as μ increases, the sharing group gains an advantage over the non-sharing group, with a different distribution of traits (Figures 3.12).

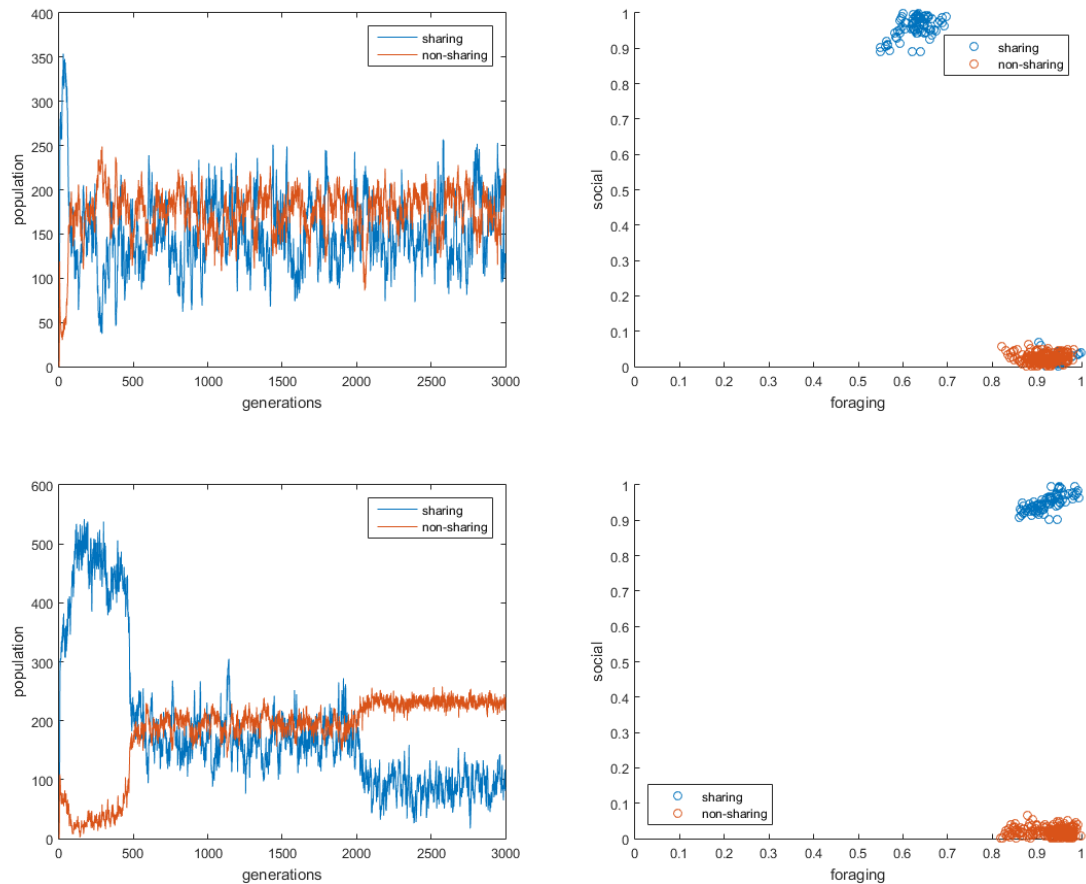


Figure 3.6 Stochastic fluctuations with $\mu = 0.01$, and 3 turns per generation. The presence of high social traits in the sharing group corresponds to greater fluctuations in the population size.

3.1.2. Extinction Rates and Final Populations. While data from sample runs show how traits affect competition between the two groups, they are only useful when both groups survive. Determining if there is an advantage to the sharing behavior requires also examining how often each group went extinct. Figure 3.13 shows the

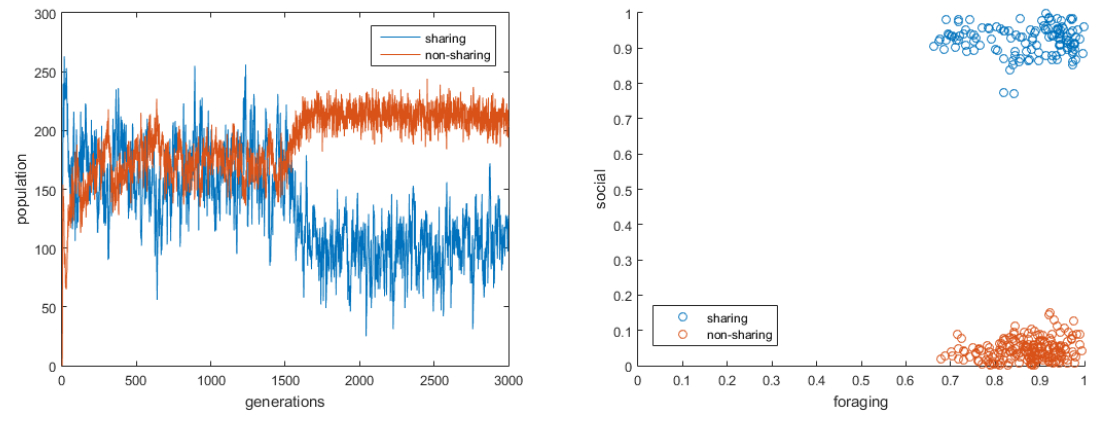


Figure 3.7 Fluctuations in population size within a single run. Parameters are $\mu = 0.03$, and 3 turns per generation.

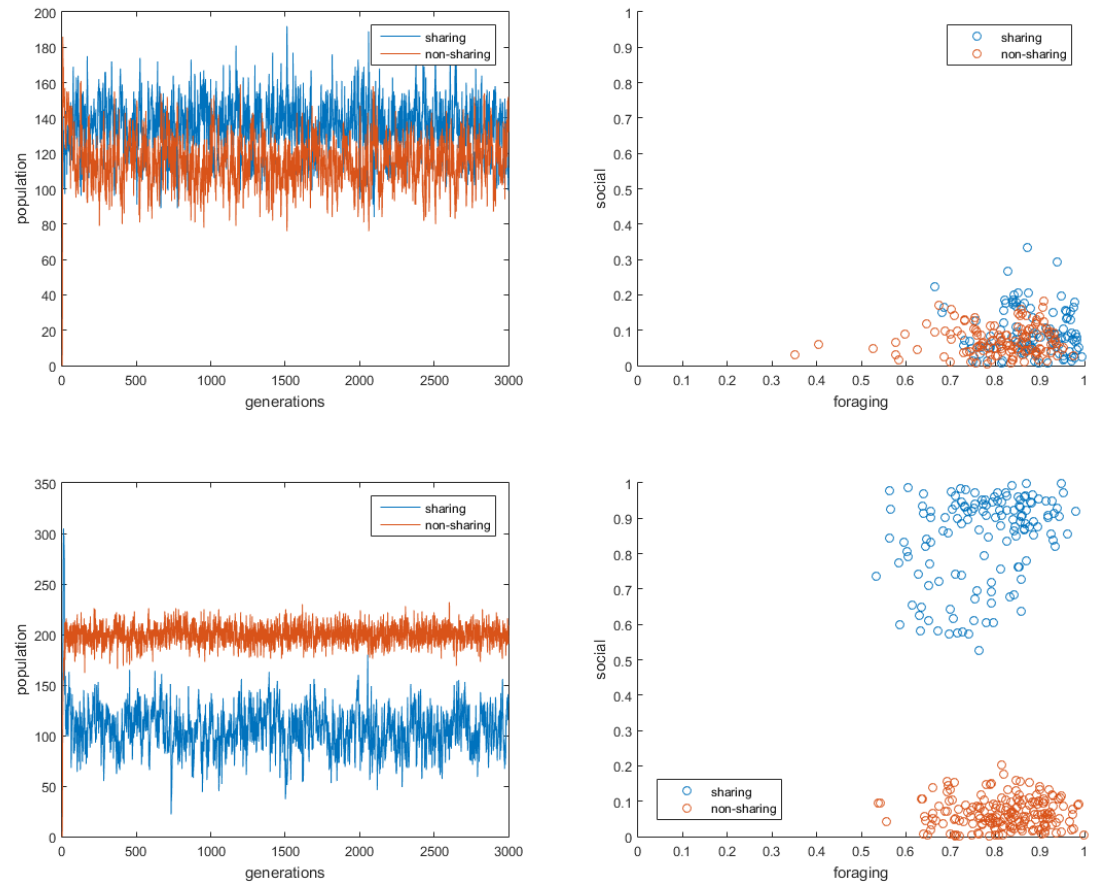


Figure 3.8 Sample runs for $\mu = 0.05$, and 3 turns per generation.

extinction rates for each turn value plotted against the mutability parameter. Extinction rates are calculated as the number of times a group went extinct from 100 simulations at each parameter combination.

The extinction rate is highest when there are few turns per generation, and at low μ values. As μ increases, the rate of extinction rapidly decreases. The most likely reason for this is that a larger μ value creates a wider range of traits, which allows each group to reach its optimal distribution more quickly. Due to the initial population being uniformly randomly distributed, more than one agent may have traits which would not be optimal in a larger population, i.e. a population that is close to the carrying capacity. Lower μ values result in the offspring of successful agents having similar trait values to the parent,

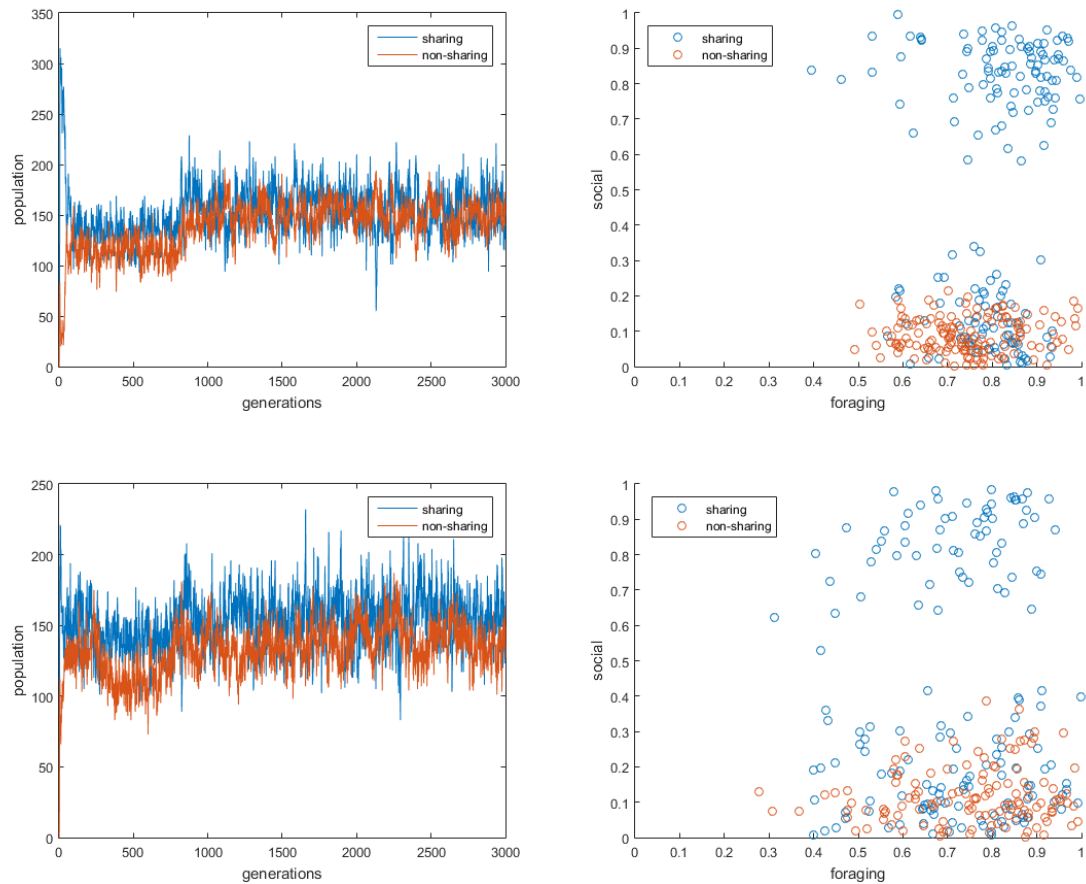


Figure 3.9 Sample runs at 3 turns per generation. Top row has $\mu = 0.07$, bottom row has $\mu = 0.09$.

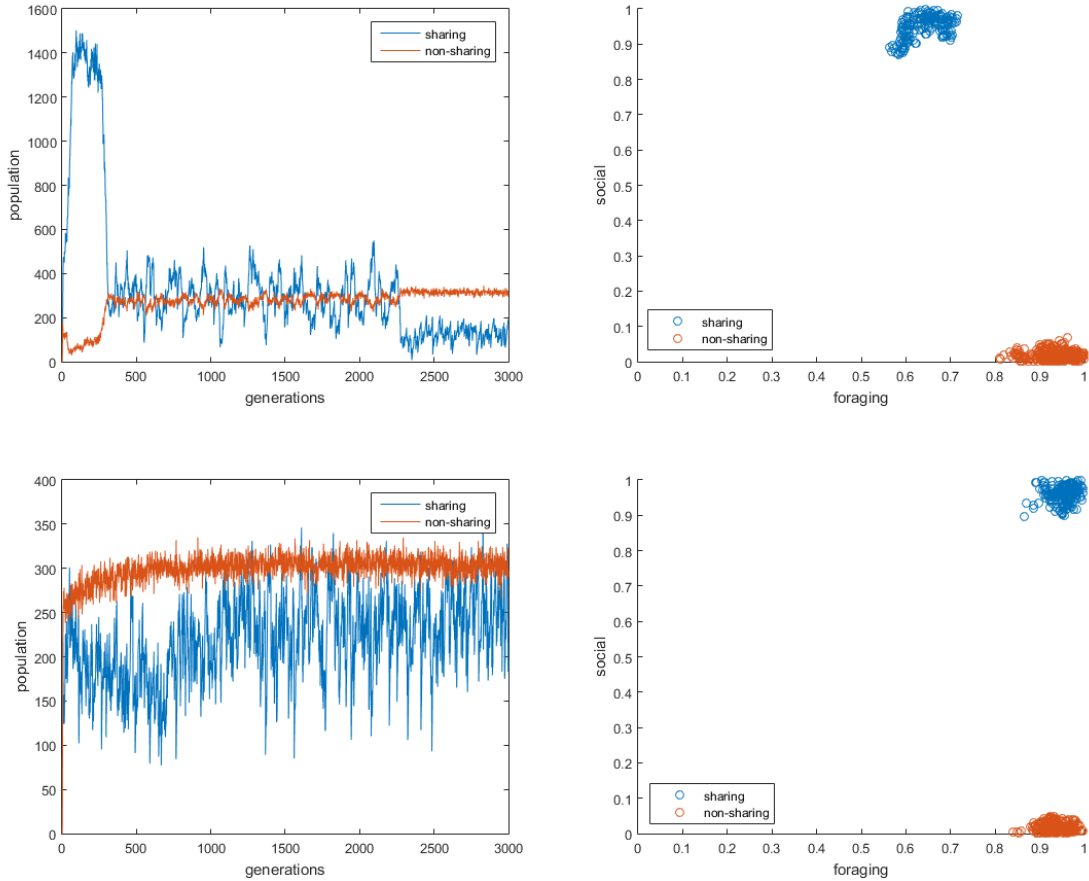


Figure 3.10 Sample runs for $\mu = 0.01$, and 4 turns per generation.

whose traits may not be viable in the next generation. As population size rapidly increases, parent populations could have more resources available to them than their offspring will have. These excess resources allow agents with traits which would be outcompeted in a larger population to have offspring. Then the offspring have similar traits, and are outcompeted in the larger population. Examining the time to extinction helps to determine if this hypothesis is correct, and Figures 3.14 & 3.15 show time-to-extinction histograms for the sharing group for $\mu = 0.01$ and 0.03 ; the sharing population always survived for higher μ values. As expected, populations overwhelmingly went extinct within the first 300 generations at $\mu = 0.01$, and all went extinct within the first 500 generations for the 1 turn case even when $\mu = 0.03$. The case with 2 turns per generation for $\mu = 0.03$ shows a far more even distribution, with some extinctions

occurring past 2000 generations. There were no extinctions at $\mu = 0.03$ for 3 or 4 turns in the sharing group.

The final factor in determining whether fitness differences exist between the sharing and non-sharing populations is to compare their average final population sizes. This is illustrated in Figure 3.16, where the average final population is plotted against the mutability parameter. Average final population values are calculated from the 3000th generation. These averages do not include runs where a group went extinct, and therefore averages are over a different amount of runs for each data point. For example, the value for the sharing group's 1 turn per generation and $\mu = 0.01$ data point was averaged over the smallest number of runs: 52, because the sharing group went extinct the other 48 times. Confirming what was suggested by the figures from sample runs above (Figures

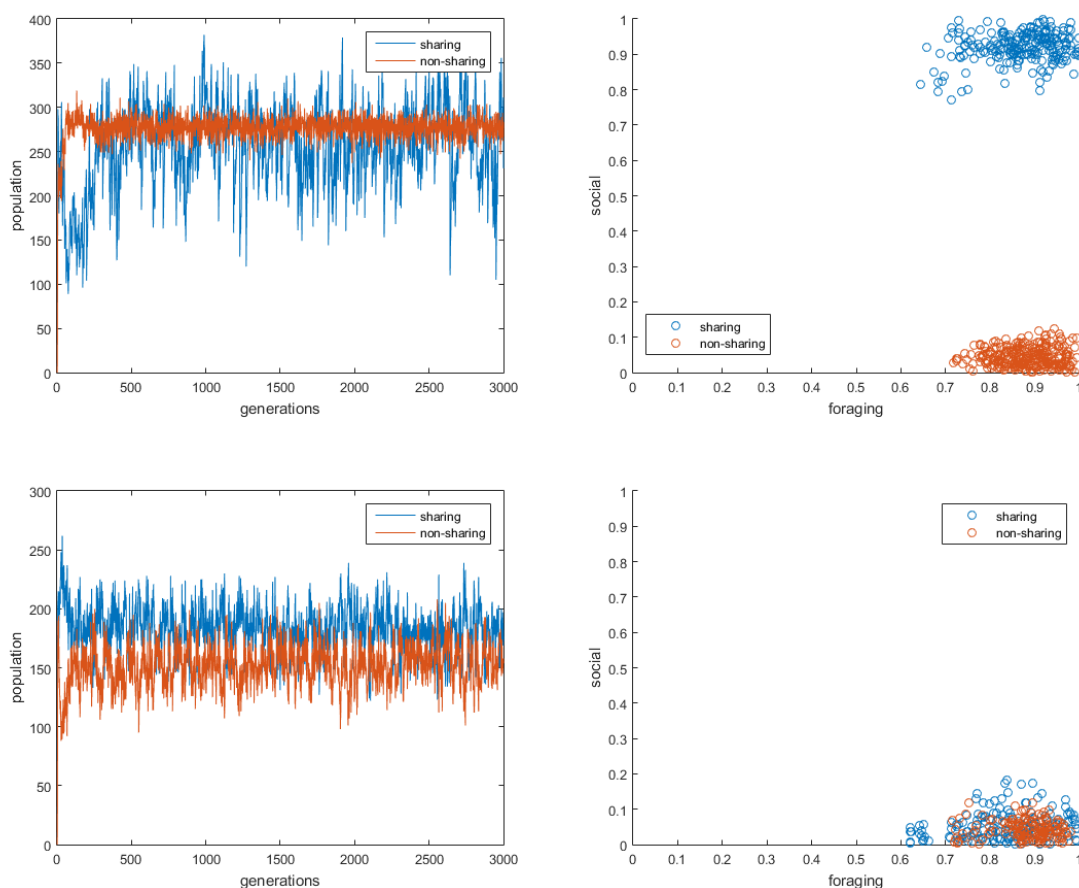


Figure 3.11 Sample runs for $\mu = 0.03$, and 4 turns per generation.

3.1-3.12), the sharing group consistently had a higher population than the non-sharing group at higher μ values, while the non-sharing group had a higher population at lower values.

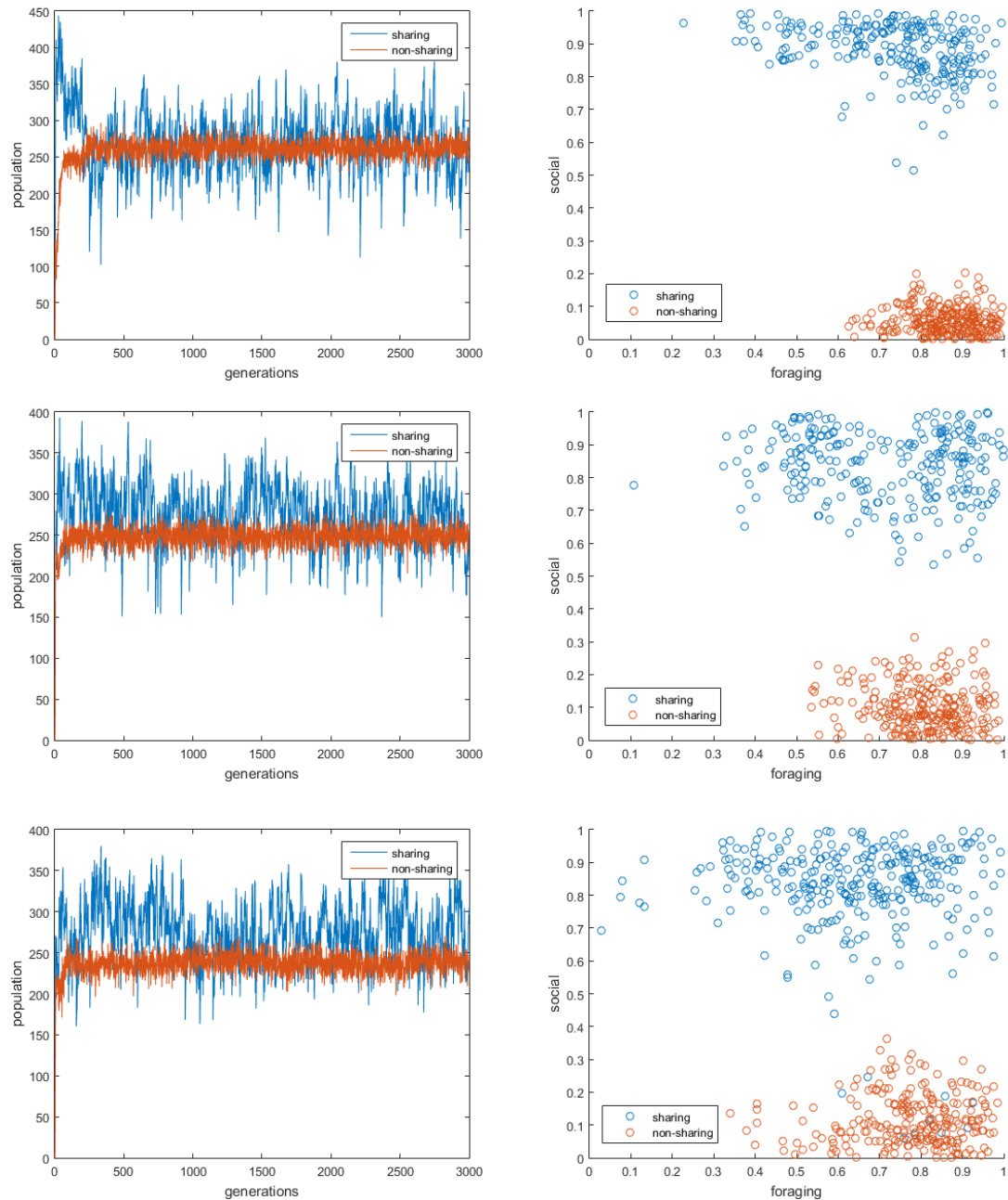


Figure 3.12 Sample runs at 4 turns per generation. From top to bottom, $\mu = 0.05, 0.07, 0.09$.

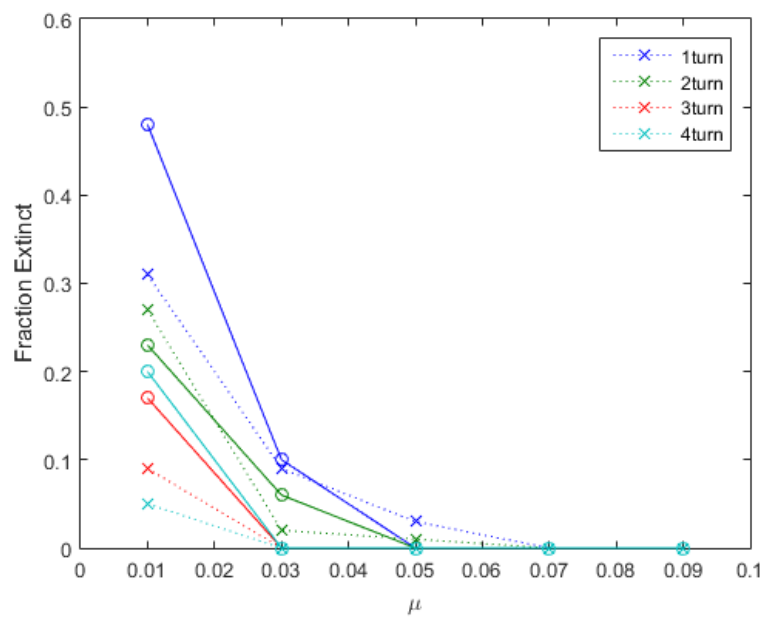


Figure 3.13 Fraction extinct vs. mutability for single resource model. Circles correspond to the sharing group, and X's to the non-sharing group.

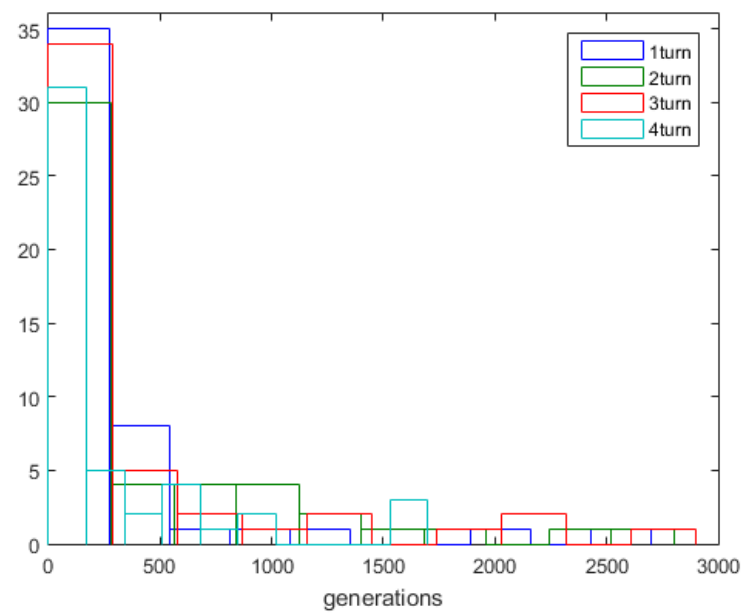


Figure 3.14 Time-to-extinction histogram for $\mu = 0.01$.

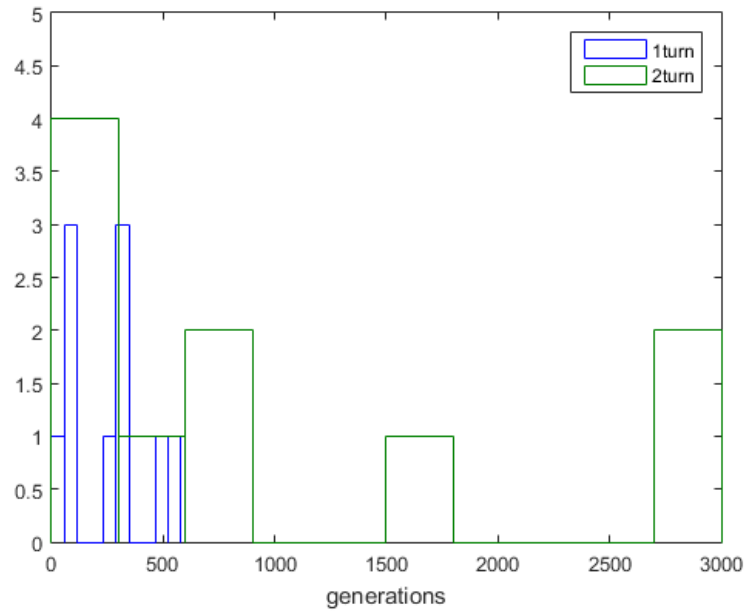


Figure 3.15 Time-to-extinction histograms for $\mu = 0.03$.

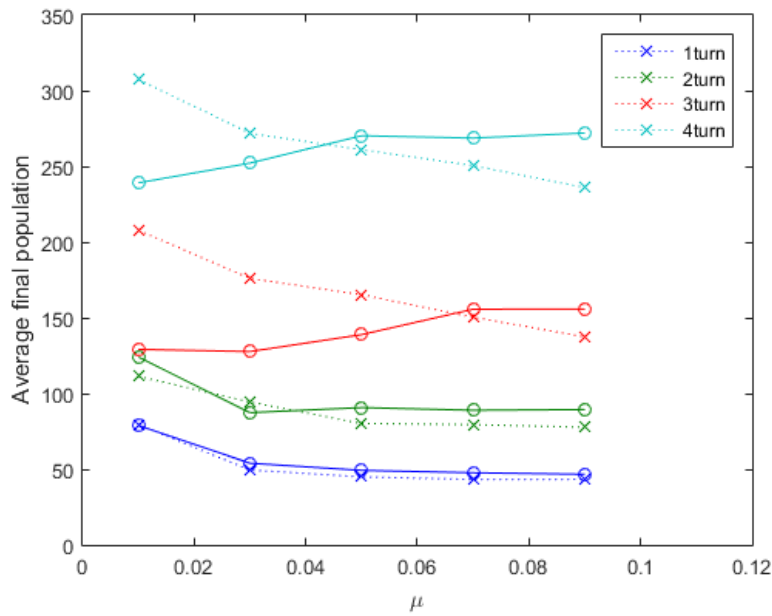


Figure 3.16 Average final population vs μ . These averages exclude runs where the groups went extinct. Sharing (circles) and non-sharing (x) groups behave differently as μ increases.

3.2. SINGLE RESOURCE WITH FORAGING RISK

The inclusion of a foraging risk increases the chance that a population can go extinct, particularly as the number of turns increases. For this reason, simulations take significantly less time than they do in the absence of the foraging risk and therefore the number of turns per generation can be increased while still allowing the acquisition of a reasonable amount of data in a short amount of time. To further lower the time required, simulations were only run for 2000 generations. For this version of the model, turns per generation ranges from 2 to 6. As above, 100 simulations were performed for each set of parameters. The foraging risk p is a flat probability for an agent to be removed when it attempts to forage. Values of p between 0.1 and 0.2 caused extinction so frequently that, for some combinations of parameters, all 100 simulations resulted in extinction. For that reason, the foraging risk p takes the values 0.01, 0.03, 0.05, 0.07, and 0.09.

3.2.1. Sample Runs with Foraging Risk. The general population behavior seen in the model without the foraging risk is unchanged. That is, when the sharing group has high foraging traits and low social traits, it ranges from exhibiting anti-phase oscillations with the non-sharing group (Figure 3.17), to gaining a slight advantage over the non-sharing group. As the number of turns increases, the size of the sharing population relative to the non-sharing population also increases (Figures 3.18-3.29). In other words, sharers with longer lifetimes have a fitness advantage. This fitness advantage also increases with μ , though the reason for this remains to be determined.

When all members of the sharing group have high social and high foraging values (Figure 3.19 & 3.20, bottom rows), the sharing group has a lower population size compared to the non-sharing group. This is likely due to the fact that agents with the sharing trait frequently give up half of their resources, resulting in a lower probability of reproduction, and lower numbers of offspring. However, this result should not be interpreted as implying that high social traits are innately disadvantageous. For example, a bimodal distribution in the social trait of the sharing group results in a similar population advantage over the non-sharing group as does the existence of exclusively low social traits (Figures 3.18, 3.19, 3.22, 3.25). In other words, it only takes some agents evolving low social and high foraging traits in order for the sharing trait to be favorable. However, this behavior is only present for 4 turns per generation or less. At 5 and 6

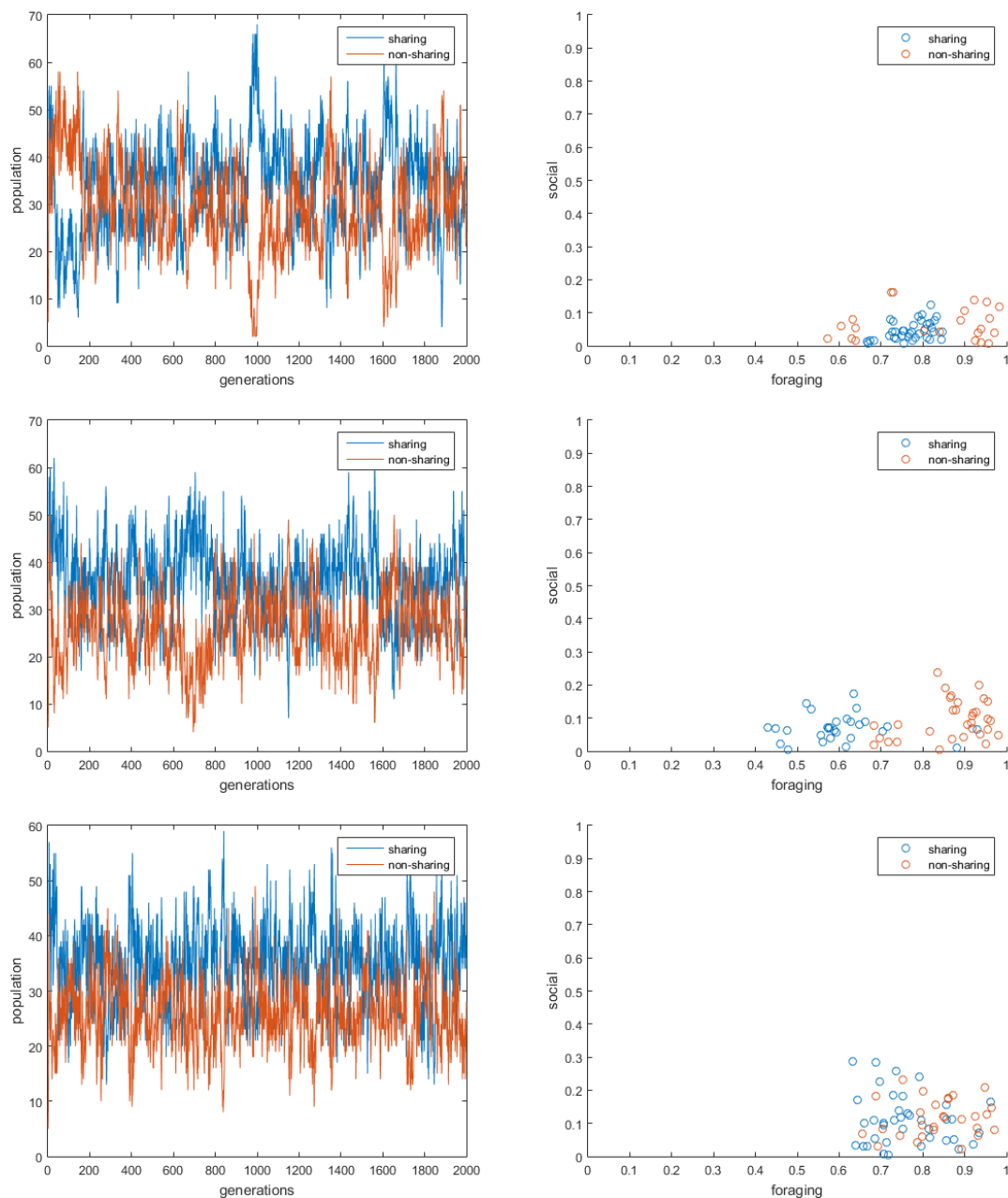


Figure 3.17 Sample runs at 2 turns and $p = 0.01$. From top to bottom $\mu = 0.03, 0.05, 0.07$.

turns, the low social, high foraging agents are no longer necessary to provide an advantage to the sharing group (Figures 3.27, 3.29). Presumably this is because the population has sufficient opportunities to acquire an amount of resources which can sustain reproduction across a significant portion of the sharing group. As the foraging risk is increased, the general behavior in trait space does not change. The population vs.

time plots show an increase in the sizes of the fluctuations in the sharing group for when there are agents with high social traits in the population.

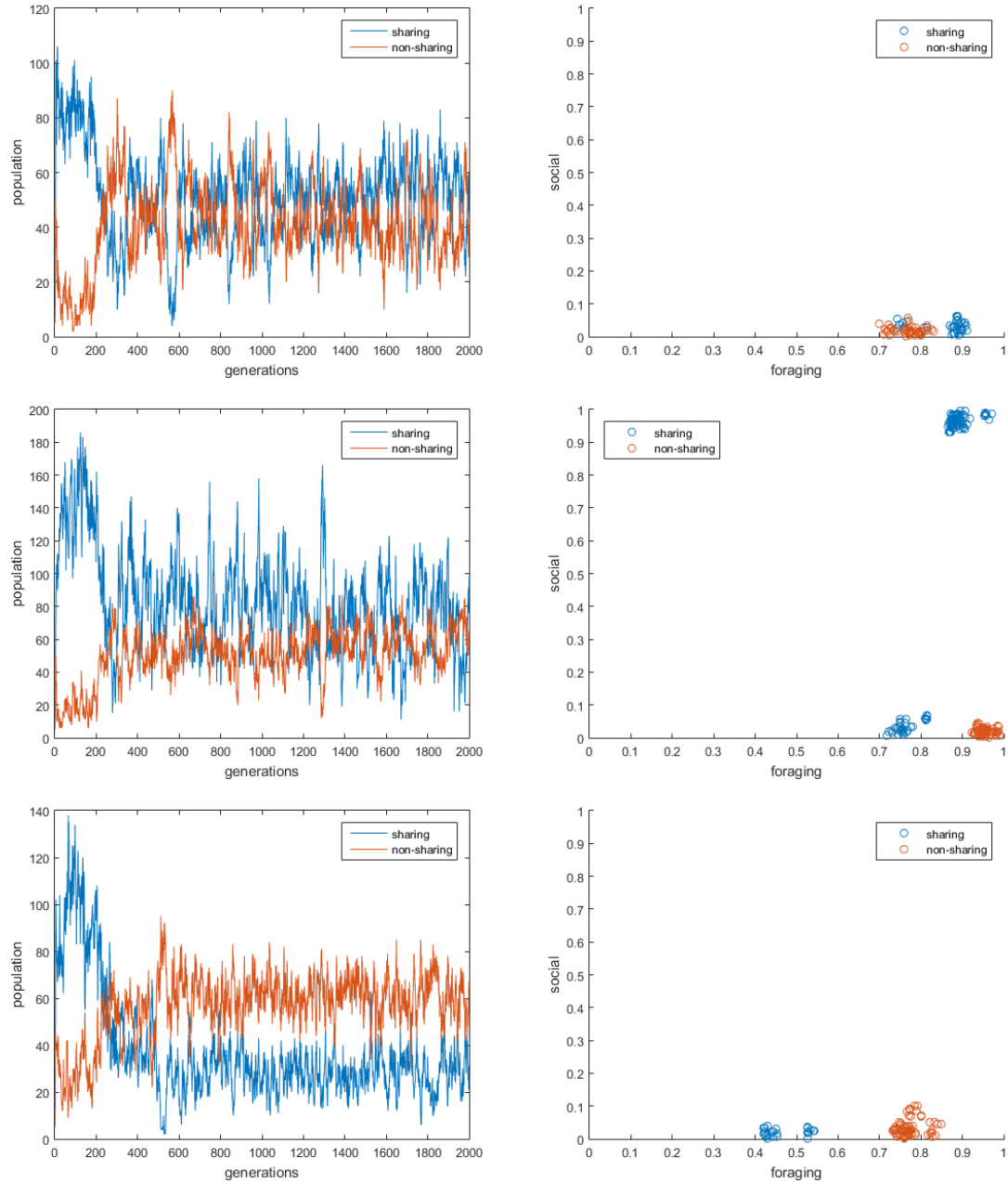


Figure 3.18 Sample runs at 3 turns, $p = 0.01$, and $\mu = 0.01$.

3.2.2. Extinction Rates and Final Populations for All p Values. The rates of extinction when the foraging risk is added differ significantly from the results in the absence of foraging risk.

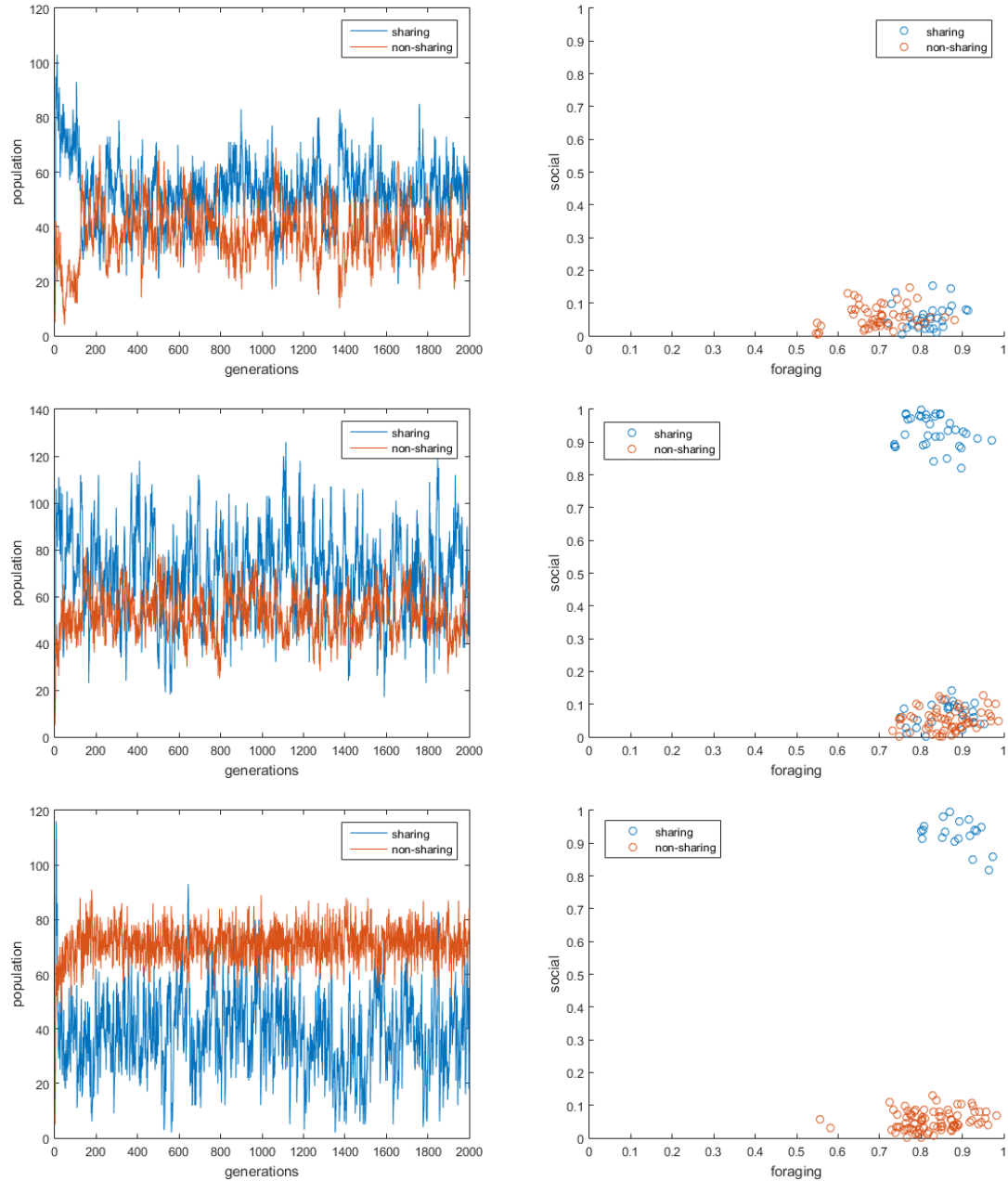


Figure 3.19 Sample runs at 3 turns, $p = 0.01$, and $\mu = 0.03$.

Starting at $p = 0.01$ (Figure 3.30), for 2-3 turns per generation, the extinction rates are similar to the basic model, where populations go extinct more frequently at lower μ values. At 4 turns, the extinction rate has a peak at $\mu = 0.03$, and at 5 or 6 turns, the peak is at $\mu = 0.05$. At $p = 0.03$, the peak extinction rates are not as obvious, and vary greatly with the number of turns (Figure 3.30). Higher values of p (Figures 3.31 & 3.32) all show peak extinction occurring at $\mu = 0.01$, but none of these data points shown reach the

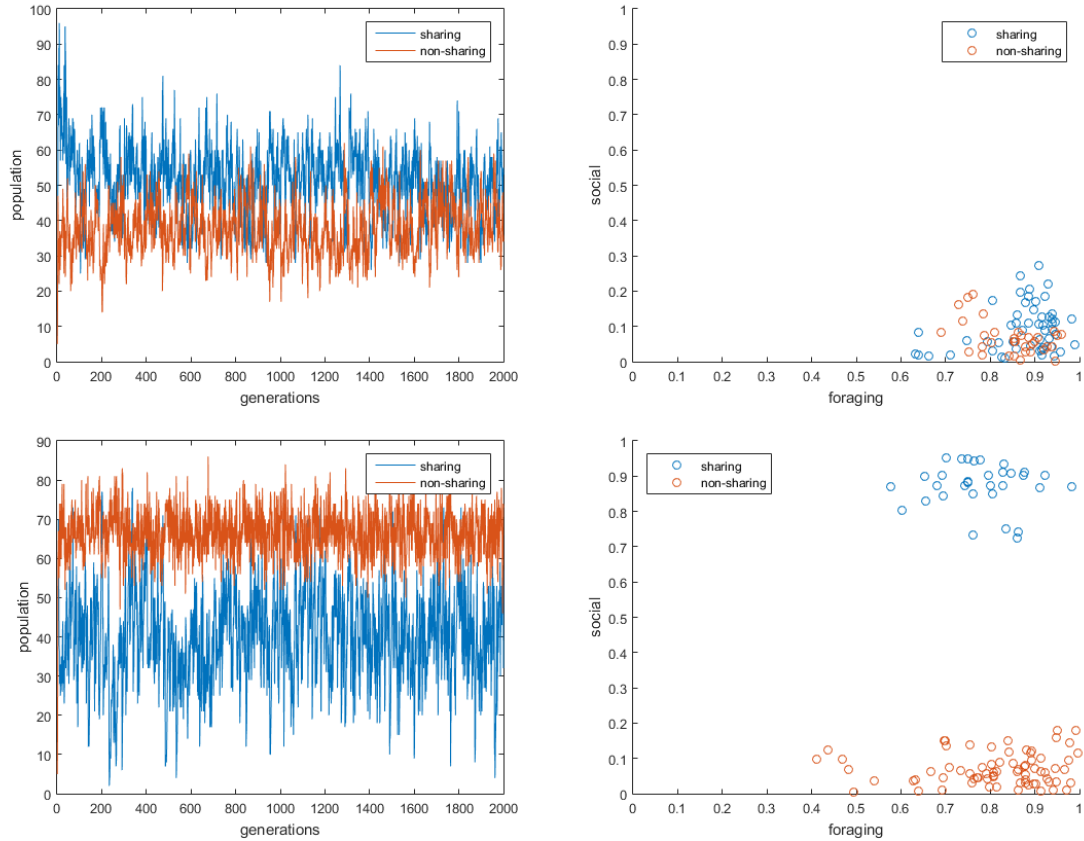


Figure 3.20 Sample runs at 3 turns, $p = 0.01$, and $\mu = 0.05$.

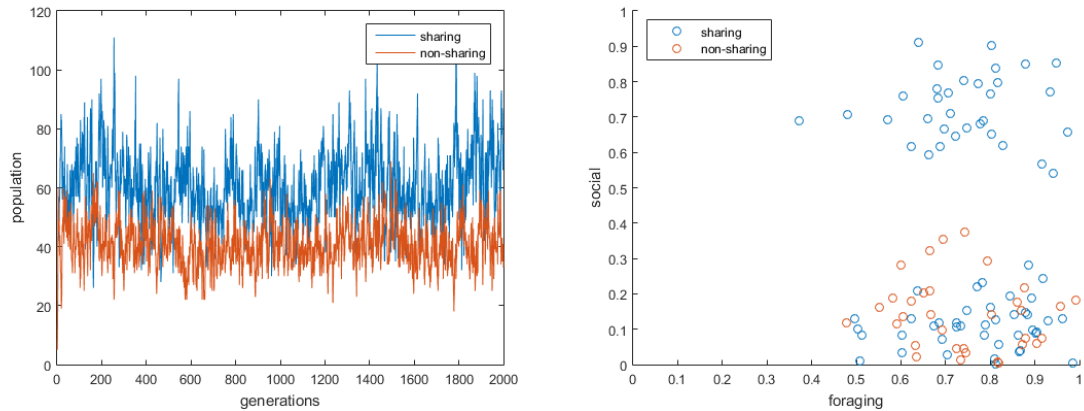


Figure 3.21 Sample run at 3 turns, $p = 0.01$, and $\mu = 0.09$.

70% or higher extinction that is seen for some values at $p = 0.01$. It is unclear exactly why extinction would occur more often at some μ values when there is a lower risk to foraging, compared to those same μ values when there is a higher risk, but it is not the only counterintuitive result. The average final populations show a significant drop at

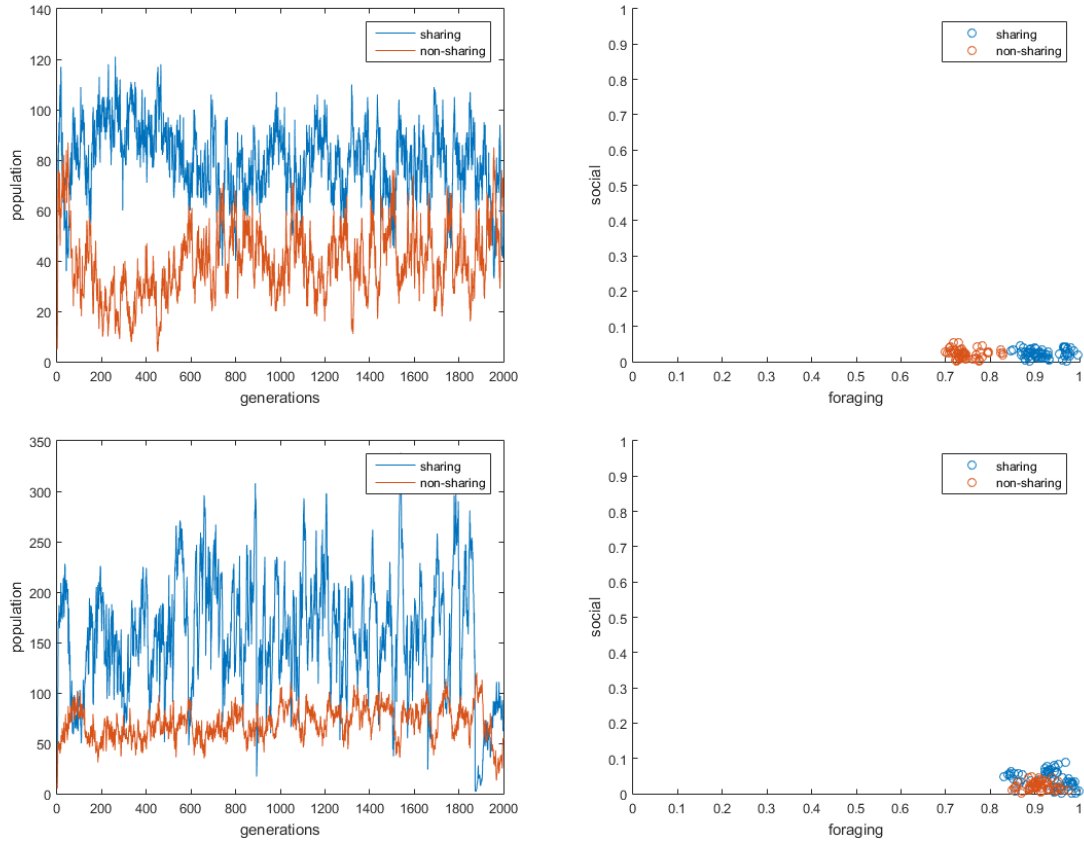


Figure 3.22 Sample runs at 4 turns, $p = 0.01$, and $\mu = 0.01$.

$\mu = 0.03$ for 4, 5, and 6 turns, compared to other μ values examined in this work, when $p = 0.01$ (Figure 3.33). This minimum value is either not as extreme, or not even a minimum for higher p values and smaller numbers of turns (Figures 3.34 - 3.35).

3.3. DISCUSSION OF RESULTS

The results presented for the single-resource model are mostly reasonable and can be easily summarized as being part of two regimes. When there are a small number of turns, there is little benefit to the social trait in the sharing group, and agents evolve to have low social, and high foraging traits, matching the behavior of the non-sharing group. As the number of turns increases, then the social trait has both a cost and a benefit to the sharing group, though the cost only seems to be relevant at low μ values. The benefit is that an agent could acquire a sufficient amount of resources from sharing, and the cost is that sharing with another agent with fewer resources will reduce the amount of resources

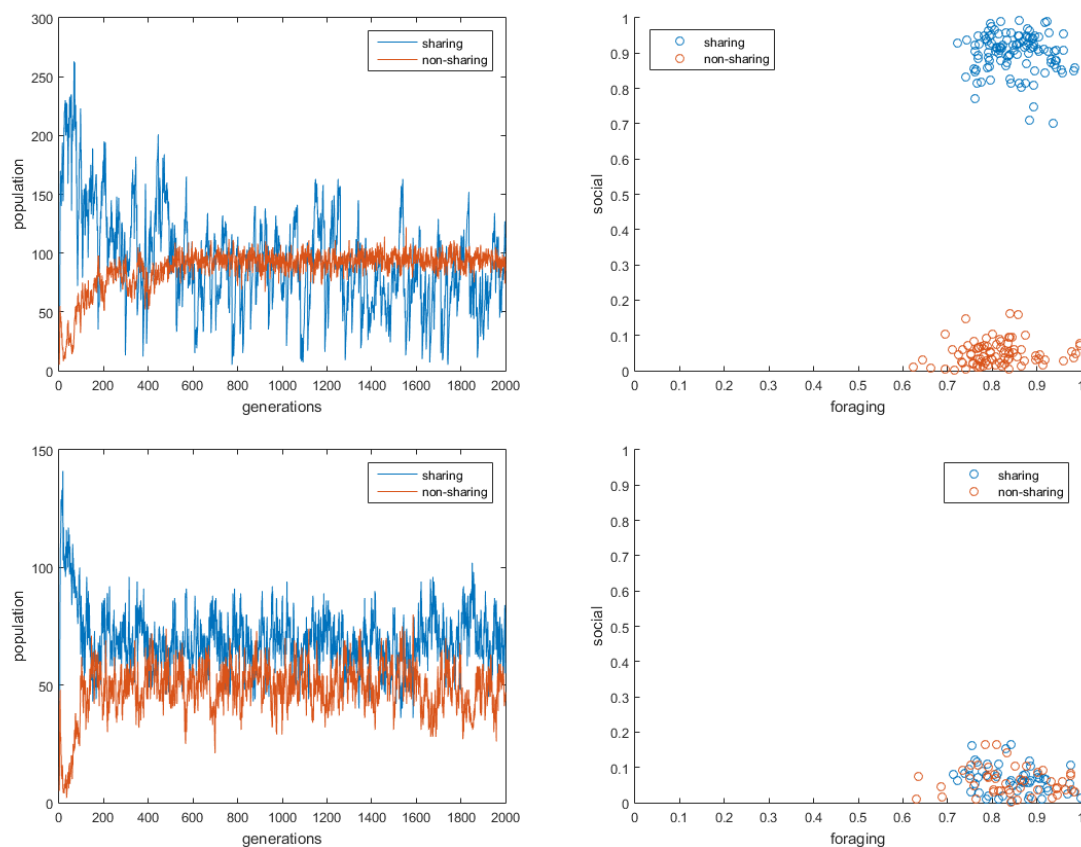


Figure 3.23 Sample runs at 4 turns, $p = 0.01$, and $\mu = 0.03$.

of the agent with the larger amount. The cost of the social trait is present when all agents in the sharing group have high social and high foraging traits, as evidenced by the sharing group having a lower population size compared to the non-sharing group. When there are some agents with low social and high foraging traits in the sharing group, then the social trait provides an advantage. This cost disappears at larger values of μ , and the social trait becomes largely beneficial, though it is the source of the large fluctuations in population size of the sharing group. The size of these fluctuations increase when the foraging risk is added, but do not further increase as the foraging risk is increased, indicating that they may be related to the extremely high rates of extinction at higher values of the foraging risk, though this result is not yet confirmed. Finally, the data from the average final populations indicate that the sharing group typically has a similar size as the non-sharing group, or even an advantage over the non-sharing group, across all parameters with only a few exceptions occurring when there is a foraging risk present. These exceptions, and some of the other inconsistent behavior that occurs when the

foraging risk is present, may be due to the small sample sizes. If simulations were run perhaps 1000 times as opposed to only 100 times, then it is possible that more consistent patterns would emerge.

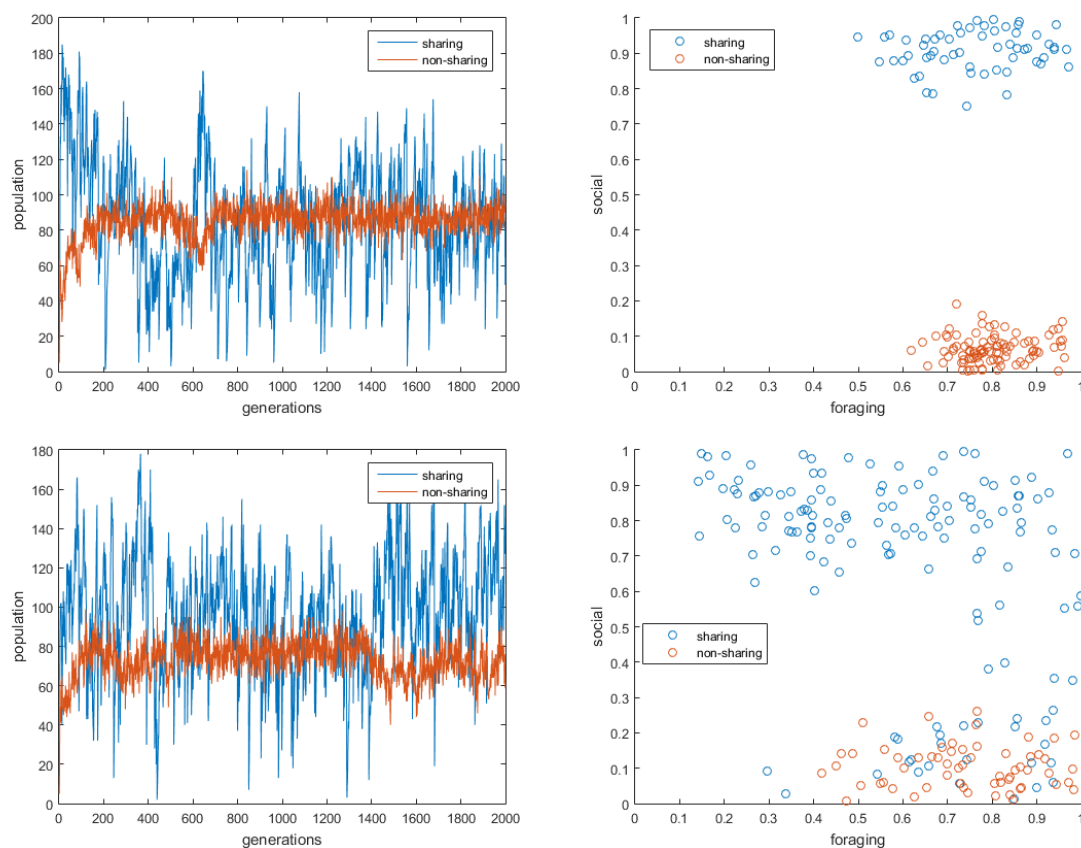


Figure 3.24 Sample runs at 4 turns, and $p = 0.01$. From top to bottom $\mu = 0.05, 0.09$.

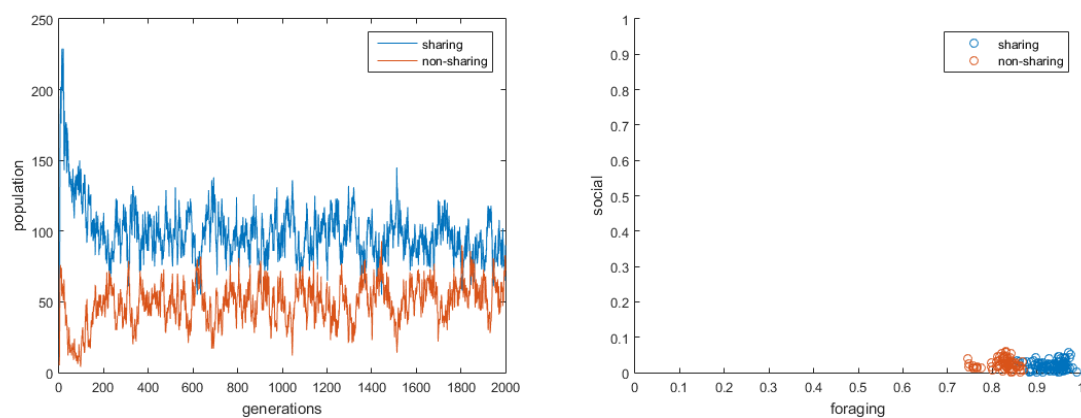


Figure 3.25 Sample runs at 5 turns, $p = 0.01$, and $\mu = 0.01$.

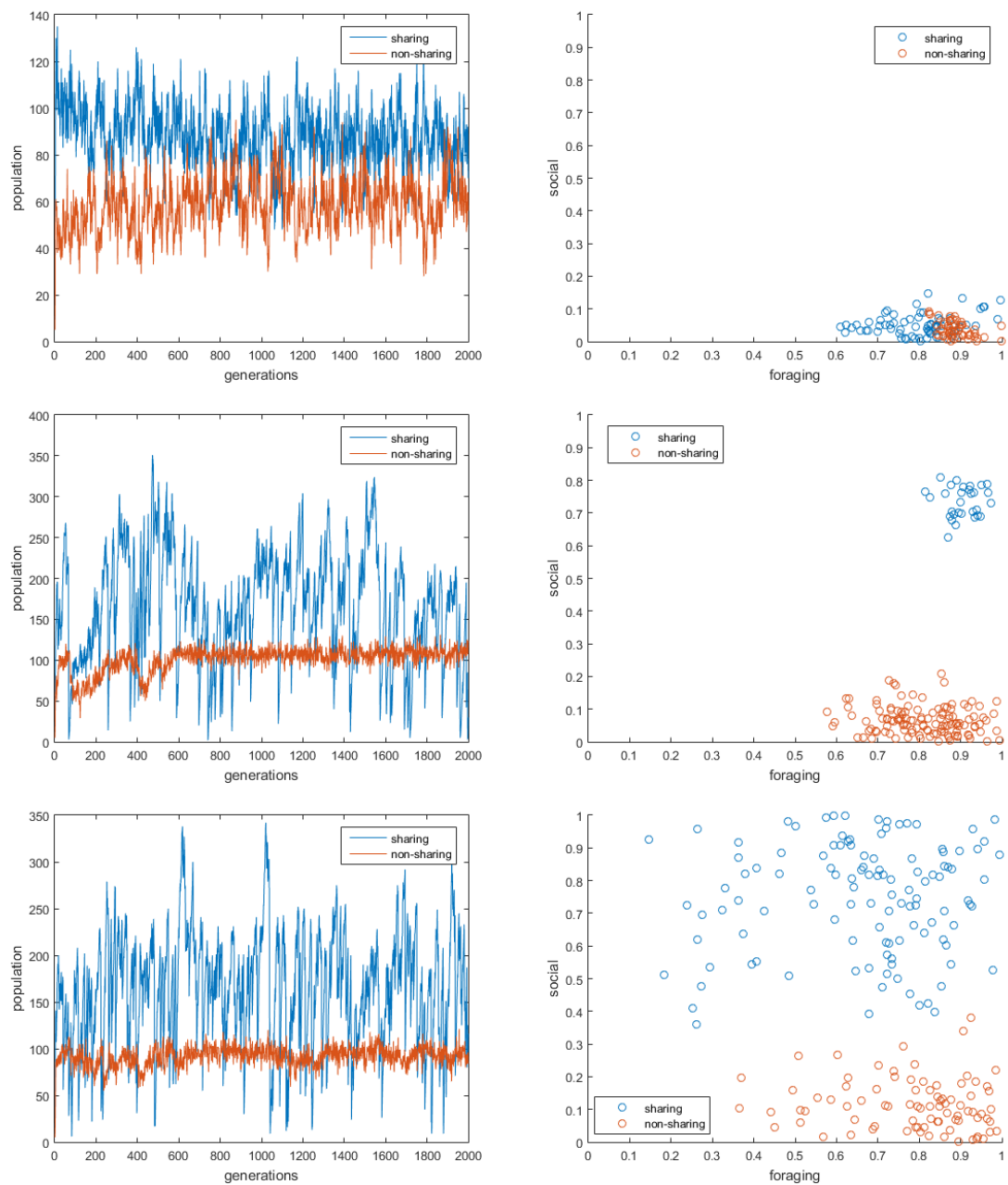


Figure 3.26 Sample runs at 5 turns at $p = 0.01$. From top to bottom $\mu = 0.03$, 0.05 , and 0.09 .

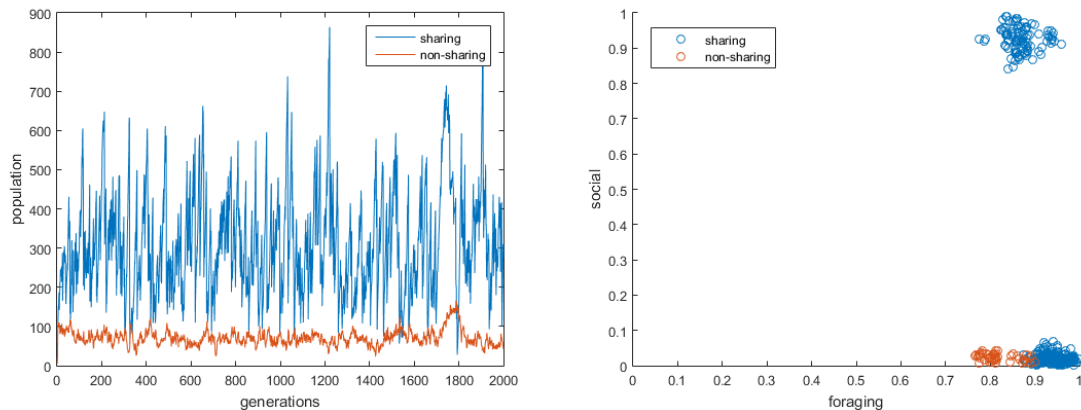


Figure 3.27 Sample runs at 6 turns, $p = 0.01$, and $\mu = 0.01$.

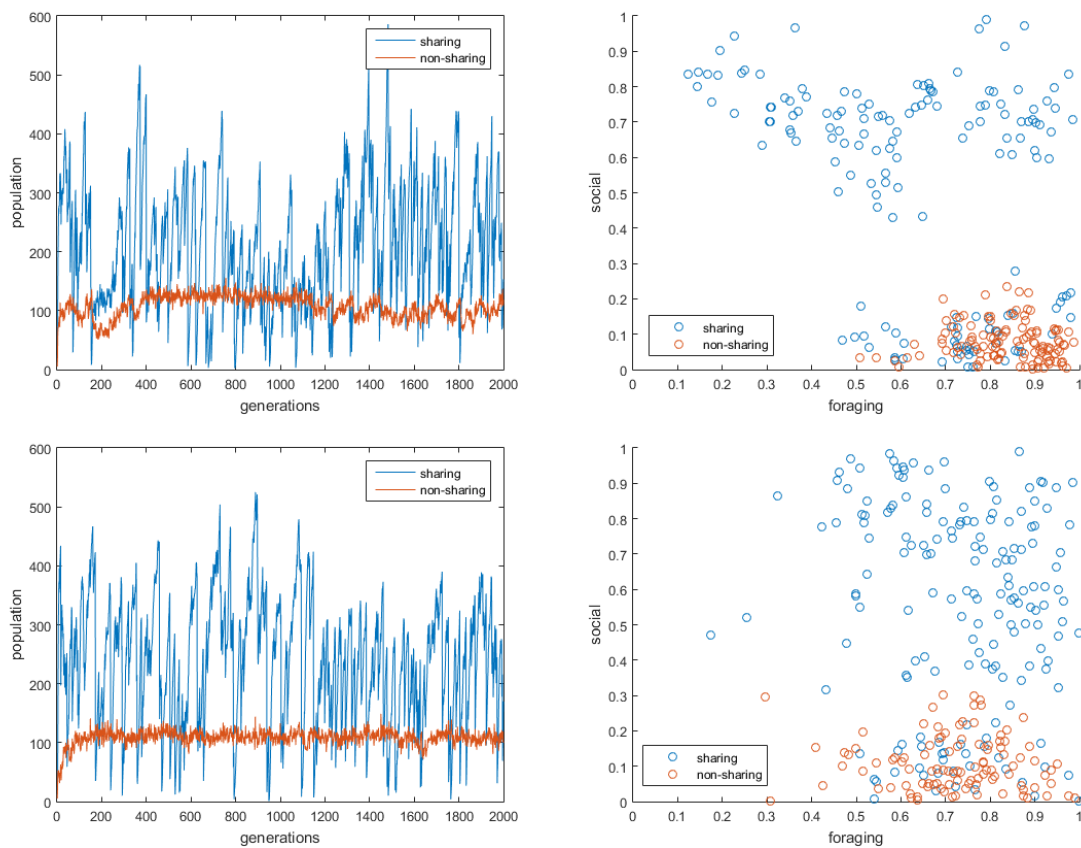


Figure 3.28 Sample runs at 6 turns at $p = 0.01$. From top to bottom $\mu = 0.05, 0.09$.

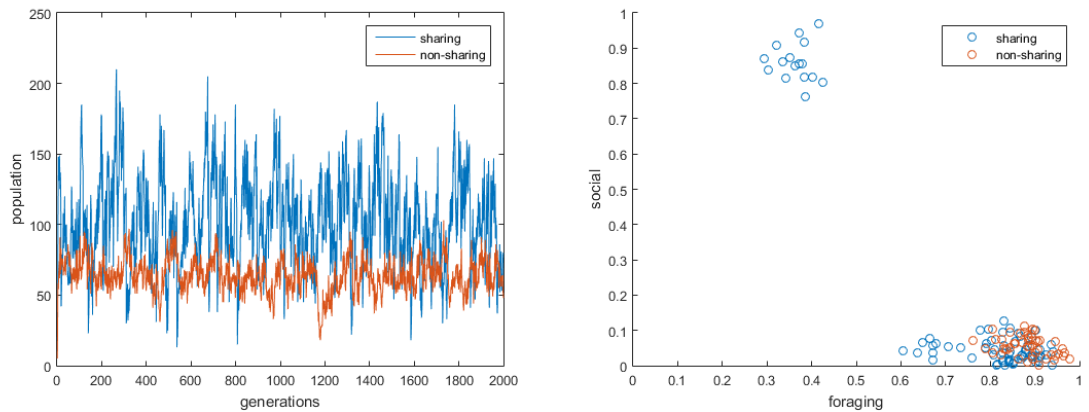


Figure 3.29 Sample run at 4 turns, $p = 0.03$, and $\mu = 0.03$.

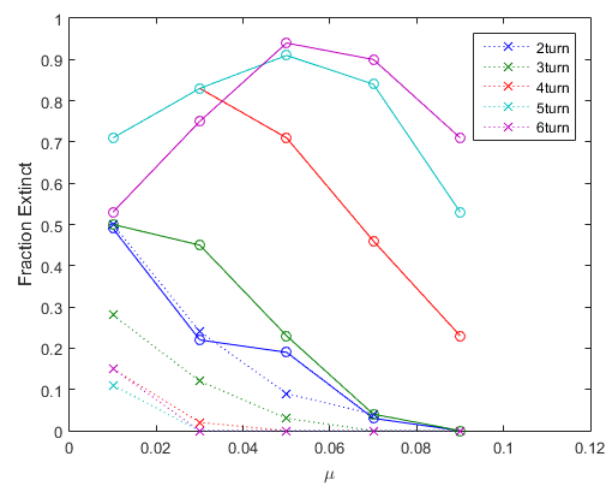


Figure 3.30 Fraction extinct at $p = 0.01$. Solid lines represent the sharing group, dotted lines are non-sharing group.

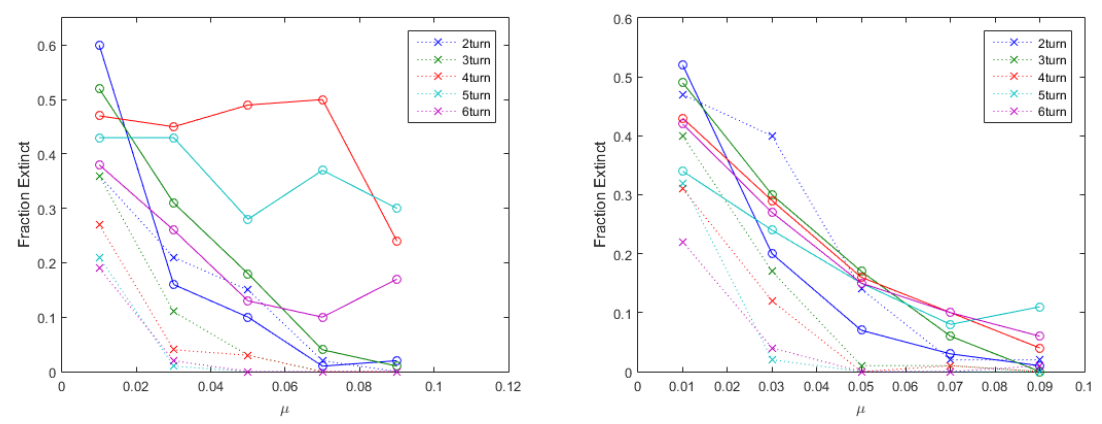


Figure 3.31 Fraction extinct at $p = 0.03$ and $p = 0.05$.

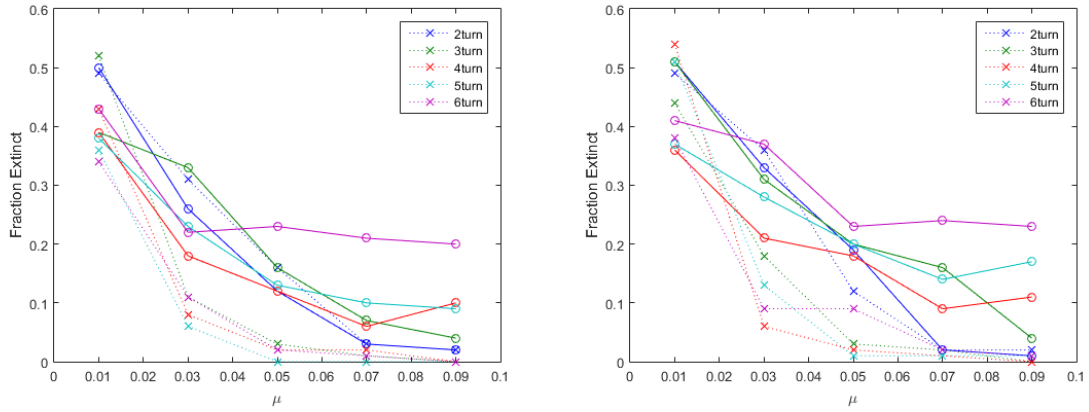


Figure 3.32 Extinction rates at $p = 0.07$ and $p = 0.09$

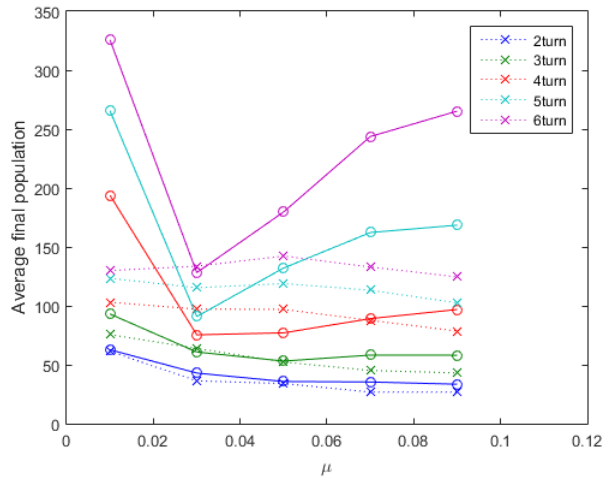


Figure 3.33 Average final populations vs. μ for $p = 0.01$.

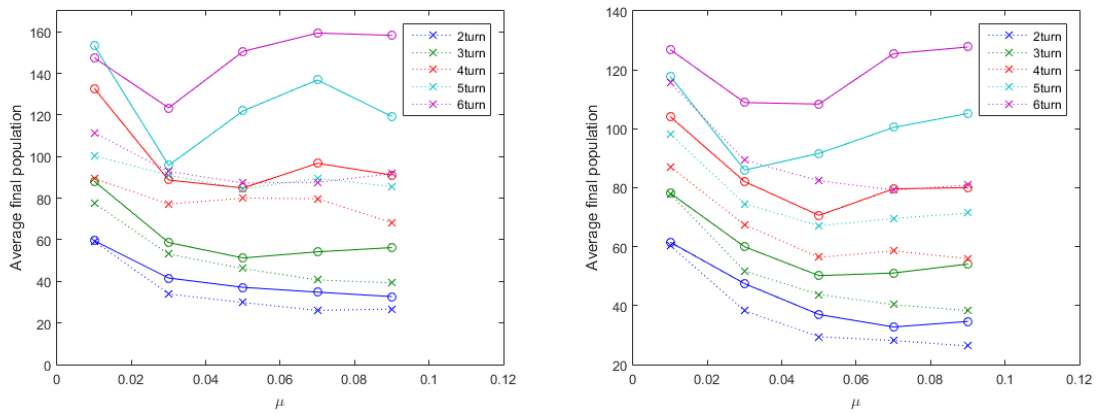


Figure 3.34 Average final populations vs. μ for $p = 0.03$ and 0.05 . Left is $p = 0.03$, right is $p = 0.05$.

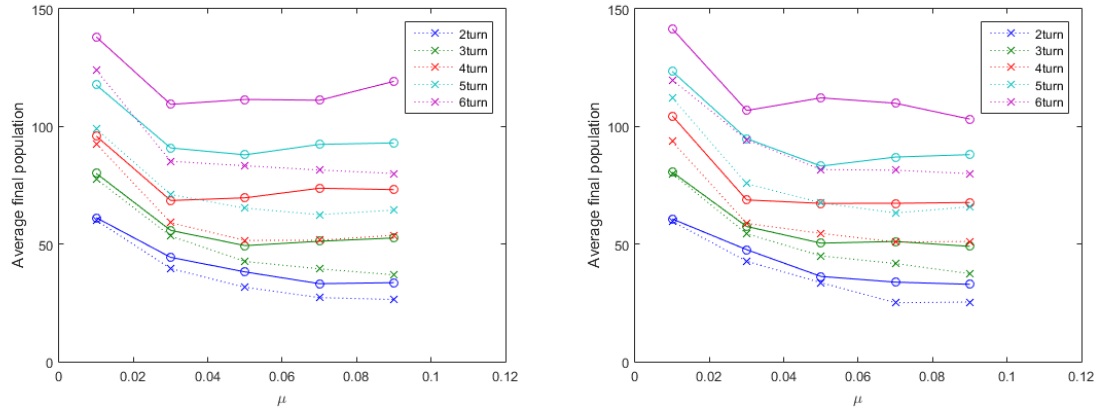


Figure 3.35 Average final populations vs. μ for $p = 0.07$ and 0.09 . Left is $p = 0.07$, right is $p = 0.09$.

4. RESULTS OF TWO-RESOURCE MODEL

What has been shown from the single resource model is arguably not a division of labor, aside from a few runs where some portion of the sharing group specialized on the social trait. Division of labor would be more convincing if the model was to evolve agents which specialize on different foraging tasks, and therefore a second resource was included to accomplish that goal.

4.1. TWO RESOURCES WITHOUT FORAGING RISK

Parameter values in this version of the model are again $\mu = 0.01, 0.03, 0.05, 0.07,$ and 0.09 , but the turns per generation is only varied from 2 to 5.

4.1.1. Sample Runs for Two-Resource Model. The presence of a third trait makes it difficult to plot both groups' traits on the same Figure. Heat maps are used to represent the social trait, and axes of figures are foraging for the survival resource and foraging for the reproduction resource (x-axis and y-axis, respectively). The non-sharing group shows more variation in this version of the model compared to the single resource model, but still has less variation than the sharing group. Agents in the non-sharing group (Figure 4.1 & 4.2) range from specializing on foraging for the survival resource, to being generalists, to everywhere in between. However, this variation in the non-sharing group is not important in determining population sizes. The primary factor which affects population size is the distribution of traits in the sharing group. For this reason, there is no comparison between sharing and non-sharing group trait distributions presented here. The remaining discussion will focus on the sharing group.

When there are only 2 turns per generation, agents in the sharing group evolve to focus on foraging for the resource necessary for survival, and have low values for the trait associated with foraging for the purposes of reproduction (Figures 4.3-4.6). The social trait can evolve with these parameters (Figures 4.4 & 4.6), though it results in a lower fitness compared to the non-sharing group when all agents are highly social (Figure 4.4).

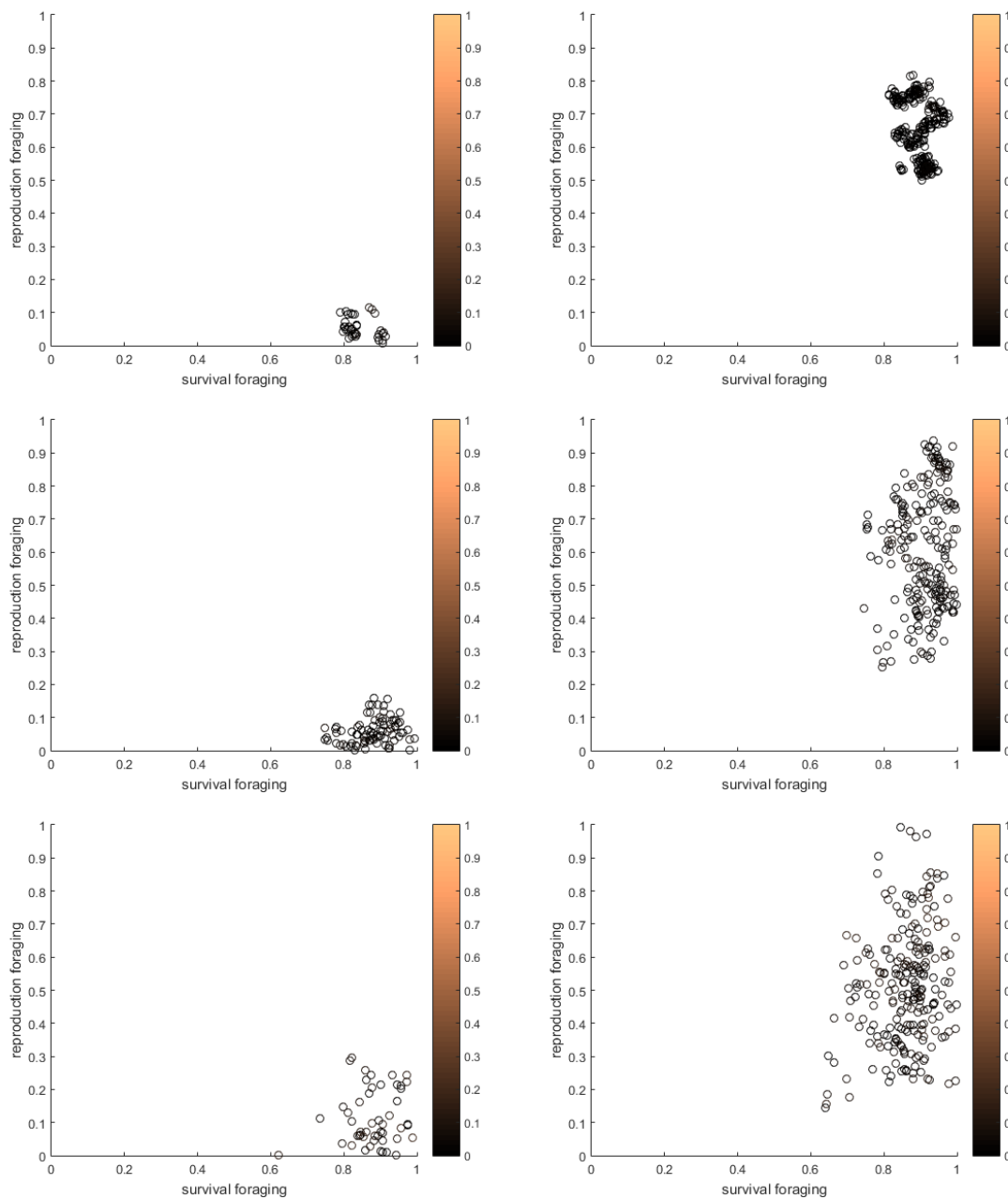


Figure 4.1 Sample trait plots for the non-sharing group. Two turns per generation (left column) and five turns per generation (right column) are shown. Intermediate values have distributions that are similar to the right column. Rows are (top to bottom) $\mu = 0.01$, 0.03 , and 0.05 .

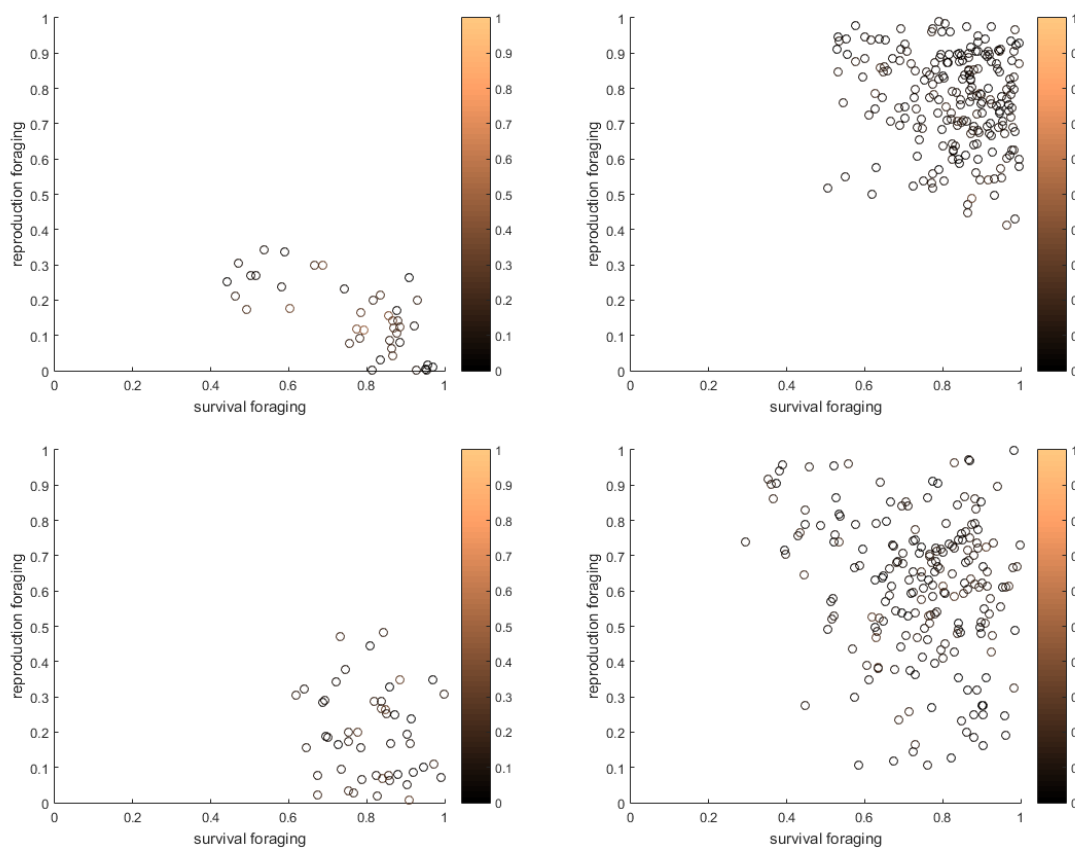


Figure 4.2 Sample trait plots for non-sharing group at $\mu = 0.07$ (top) and 0.09 (bottom). Left column has two turns per generation, and right column has five turns per generation.

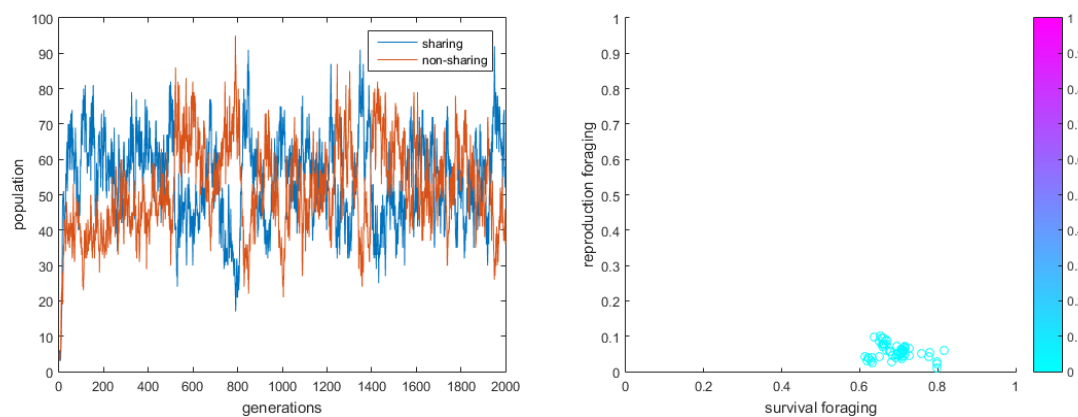


Figure 4.3 Sample run for 2 turns, $\mu = 0.01$. Trait plot for sharing group (right) with heat map for social trait, from cyan (low) to magenta (high).

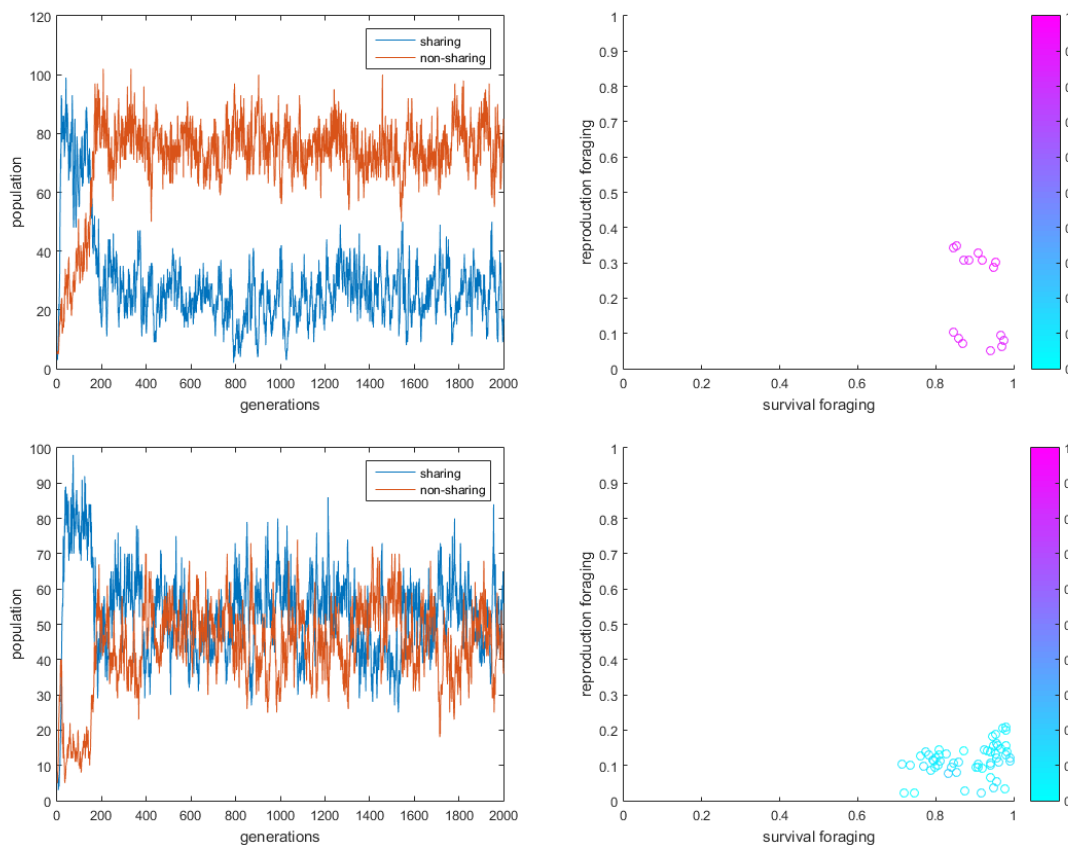


Figure 4.4 Sample runs at 2 turns, $\mu = 0.03$. Note the high social trait values – and low sharing population size – in the first row.

Increasing the number of turns per generation to 3 turns enables the social trait to appear more frequently (Figures 4.7-4.11), and it can be seen that the social trait alone is not sufficient to cause a fitness disadvantage (Figure 4.8). In fact, if highly social agents exist alongside non-social agents (Figures 4.8-4.11), the sharing group actually gains a noticeable fitness advantage. Presumably, the cause of this advantage is that the agents with high values of both foraging traits are able to consistently procure resources which are then distributed among the rest of the population by the agents with the high social traits.

At 4 turns per generation, the sharing group has a consistent fitness advantage over the non-sharing group (Figures 4.12-4.14), regardless of the exact trait distribution, though having social agents present makes this advantage far more noticeable. The case where the sharing group has a cluster of agents with low social traits and high values in

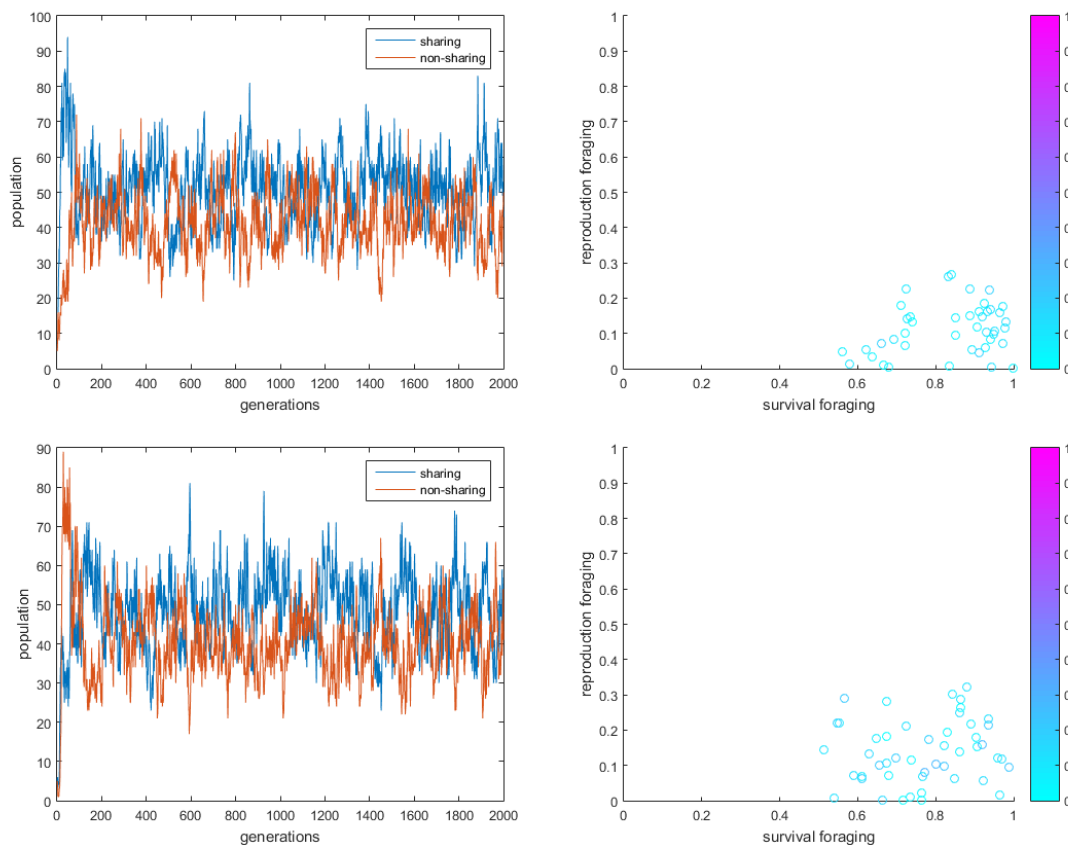


Figure 4.5 Sample runs at 2 turns, $\mu = 0.05$ (top) and 0.07 (bottom).

both foraging traits, and also a cluster with mid to low foraging and high social traits (Figure 4.12), produces a population which is larger than other distributions, and at any other combination of parameters.

Five turns per generation looks much like 4 turns (Figures 4.15-4.17), with an abundance of social agents in nearly every simulation. The same general behavior holds as well. A sharing group that contains both agents with large social trait values and agents with large trait values in both foraging traits, leads to the largest population sizes.

4.1.2. Extinction Rates and Average Final Populations. The figures for extinction rates and average final populations support some of the information seen in the population vs. time plots from sample runs. Extinction rates are again calculated as the number of times a population went extinct out of 100 runs. Average final populations are calculated by the population size at the 2000th generation and averaged over the number of runs where the group did not go extinct.

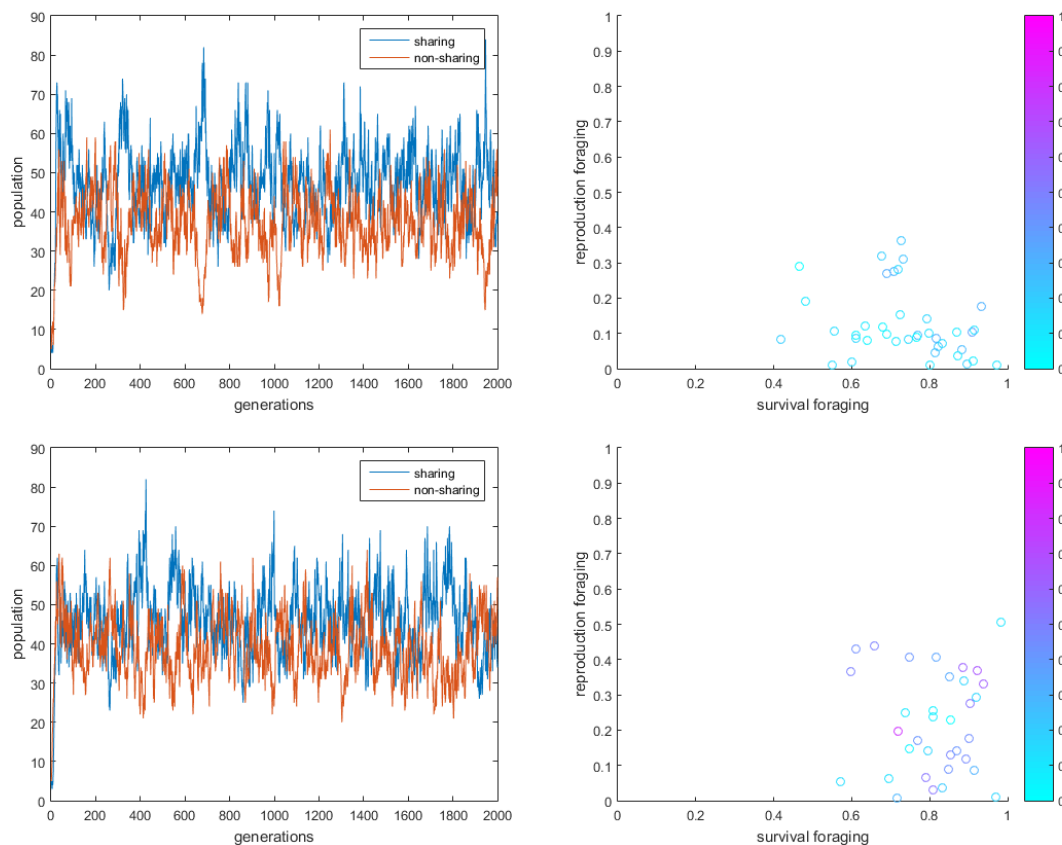


Figure 4.6 Sample runs at 2 turns, $\mu = 0.09$.

For 2 turns, the sharing group has roughly the same average final population as the non-sharing group, but goes extinct a little less frequently. The extinction rates decrease as μ increases (Figure 4.18). At 3 turns, the sharing group has a slightly larger average population and has lower extinction rate at $\mu = 0.01$, but rates for larger μ values, are similar between the two groups. When there are 4 or 5 turns, the sharing group has both a larger average final population and a higher extinction rate than the non-sharing group. The average final populations also decrease as μ increases, though they decrease faster for larger numbers of turns per generation.

4.2. TWO-RESOURCE MODEL WITH FORAGING RISK

With two resources, a foraging risk could be added in two different ways. There could be is a risk to foraging of any kind, so that an agent engaging in the act of foraging for either resource has a probability of death. Alternatively, there could be a risk

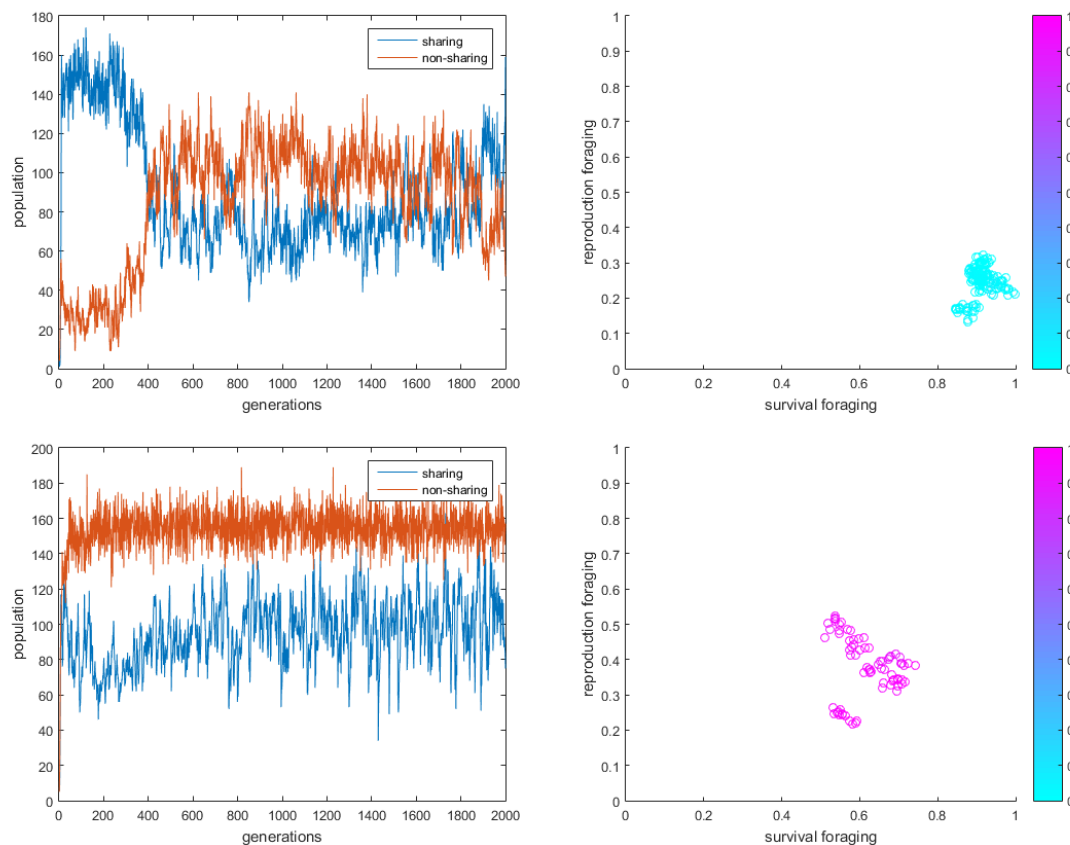


Figure 4.7 Sample runs in the two-resource model at 3 turns, $\mu = 0.01$.

associated with only one type of resource, either the resource necessary for survival or the one necessary for reproduction. Because the results from the model without a foraging risk indicate that agents typically evolve to focus on the survival resource, it is that resource which has been chosen to have a risk associated with it.

4.2.1. Sample Runs for Two-Resource Model with Foraging Risk. Adding a foraging risk to the two-resource model resulted in two notable changes in trait distributions. The first is that the range of parameters over which the social trait has a bimodal distribution increases. Without the foraging risk, this bimodal distribution appears at $\mu = 0.03, 0.05, 0.07,$ and 0.09 for 3 turns per generation, and $\mu = 0.01$ for 4 and 5 turns per generation. When the foraging risk is added, at $p = 0.01$ and higher, the bimodal distribution also appears at $\mu = 0.01$ for 3 turns per generation (Figure 4.19), so that all values of μ examined in this work can produce a bimodal distribution in the social trait at 3 turns per generation. For $p = 0.03$ and higher, the bimodal distribution also appears at $\mu = 0.03$

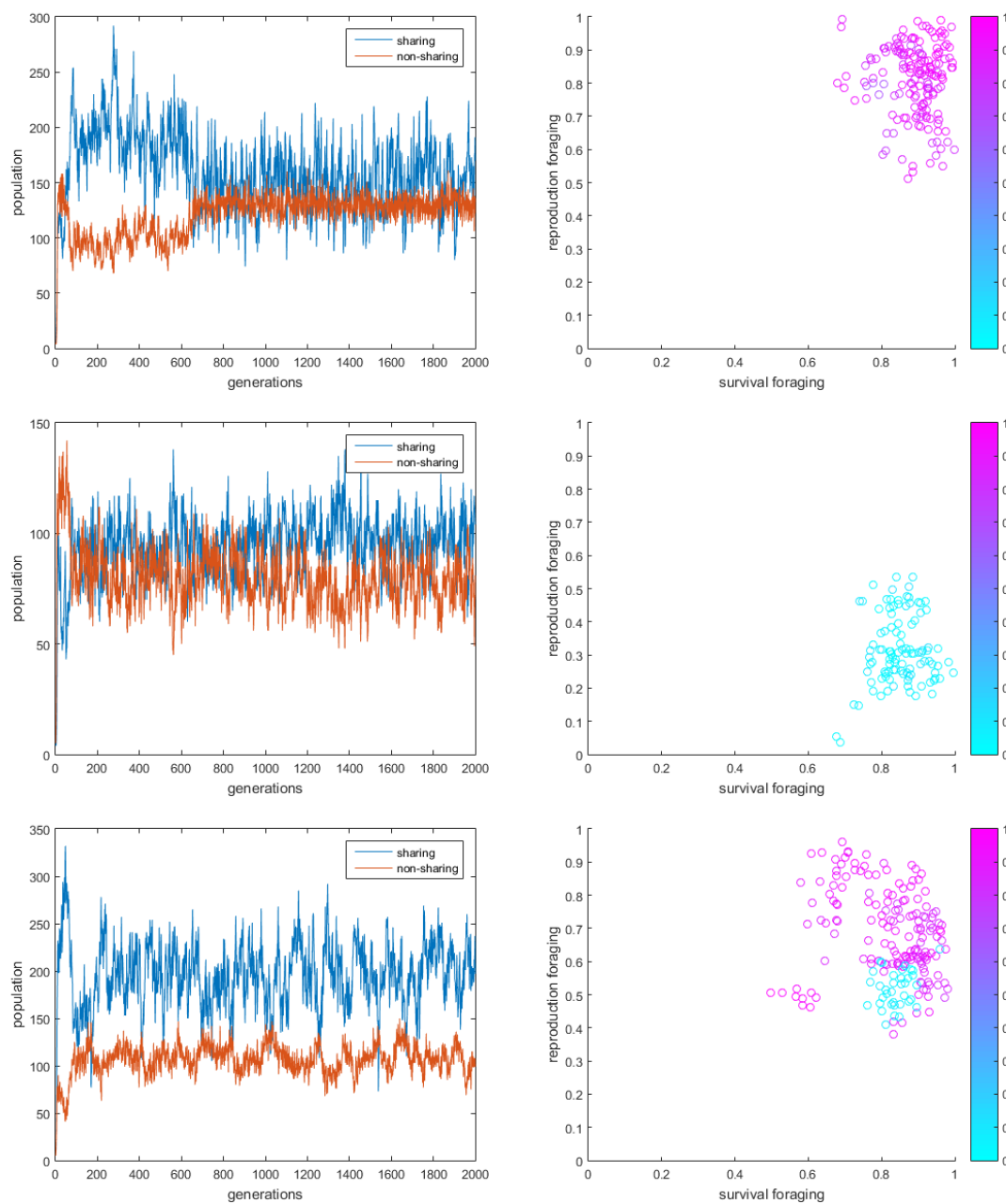


Figure 4.8 Sample runs at 3 turns, $\mu = 0.03$. A distribution which is bimodal in the social trait (bottom row) is possible, but this behavior does not always occur.

(Figure 4.19), 0.05, and 0.07 (Figure 4.20) for 4 turns per generation. At $p = 0.05$ and higher, the bimodal distribution in the social trait also occurs at $\mu = 0.09$ for 4 and 5 turns per generation.

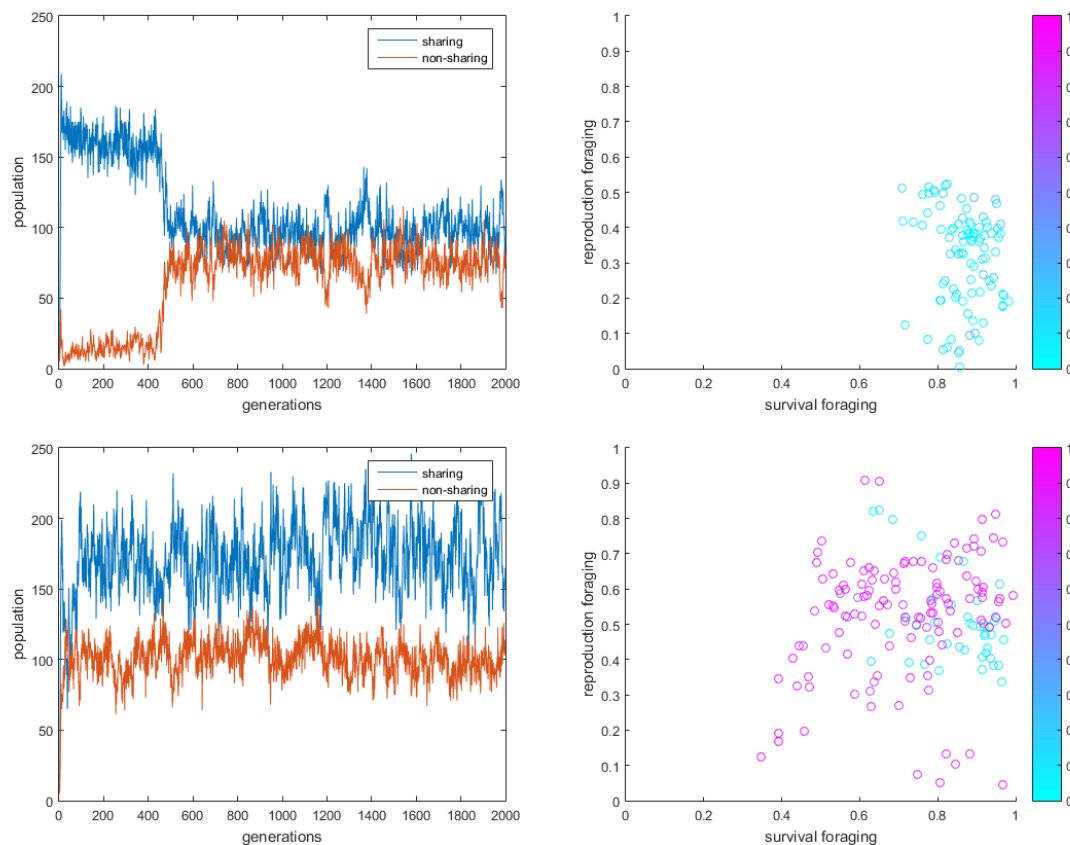


Figure 4.9 Sample runs at 3 turns, $\mu = 0.05$.

Adding a foraging risk to the two-resource model alters extinction rates by making them both higher and more subject to variance. In particular, the extinction rates for 2 turns at values $p = 0.05, 0.07$, and 0.09 (Figures 4.21-4.23) show no patterns at all.

Running more than 100 simulations would likely be necessary to determine any consistency to these extinction rates. Average final populations show the same general behavior as seen without the foraging risk, albeit with more variance. The sizes of the final populations are lower with the foraging risk, particularly when there are 5 turns per generation. They also decrease as the foraging risk increases, which is to be expected.

4.2.2. Summary of Results from the Two-Resource Model. The inclusion of a second unique resource to the model altered the results in significant ways. The single-resource model showed that the presence of high social traits in the sharing group was generally a disadvantage unless it coincided with low social and high foraging traits. In

the two-resource model, the presence of high social traits in the sharing group is still a disadvantage if the social agents also have low foraging traits, but if the sharing group has high values for both foraging traits, then the presence of the social trait is beneficial.

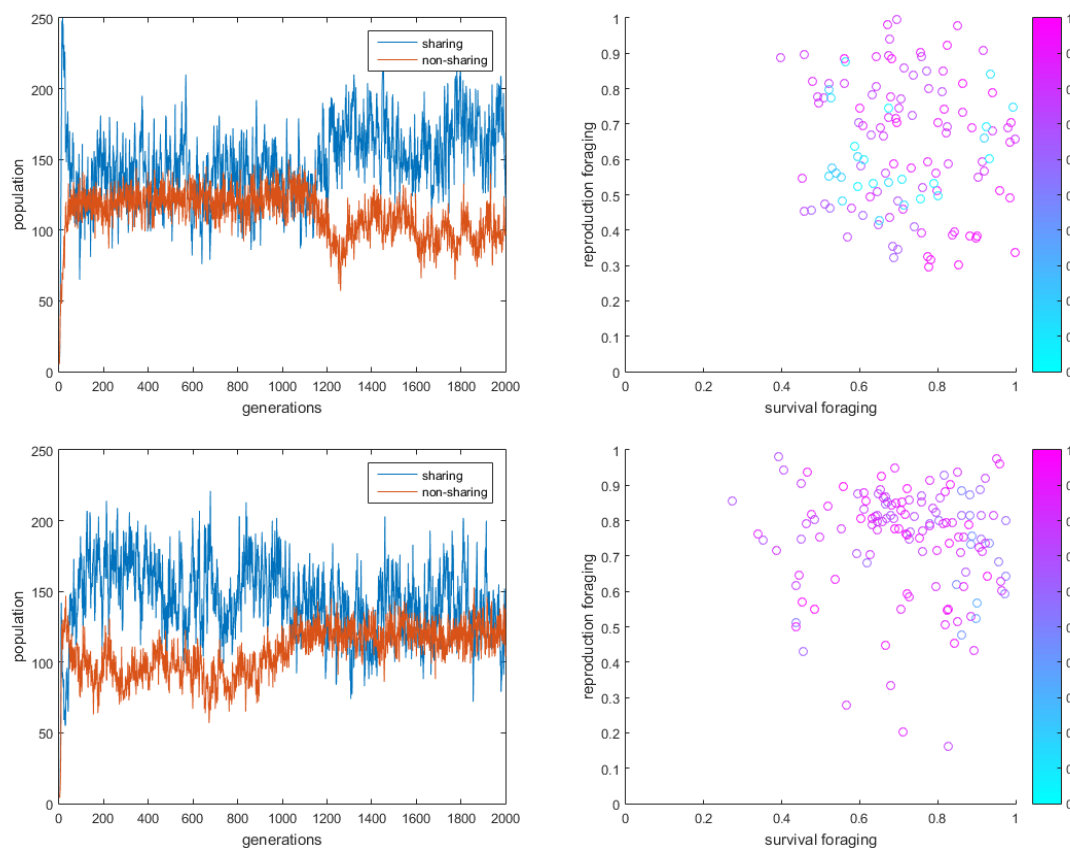


Figure 4.10 Sample runs at 3 turns, $\mu = 0.07$.

Distributions in some runs contained both a non-social group of foragers as well as a highly social group of non-foragers, representing the most convincing example of task specialization produced by any version of the model. This result demonstrates that division of labor via phenotypic specialization can evolve without task-switching costs, under the proper conditions.

The addition of a foraging risk in the two-resource model had a very small impact on the results aside from an increased variance in the extinction rates. Comparing this result with the single-resource model, it seems that decoupling the benefits of resource acquisition into two separate resources required for successful reproduction provided a buffer against the effects of the foraging risk.

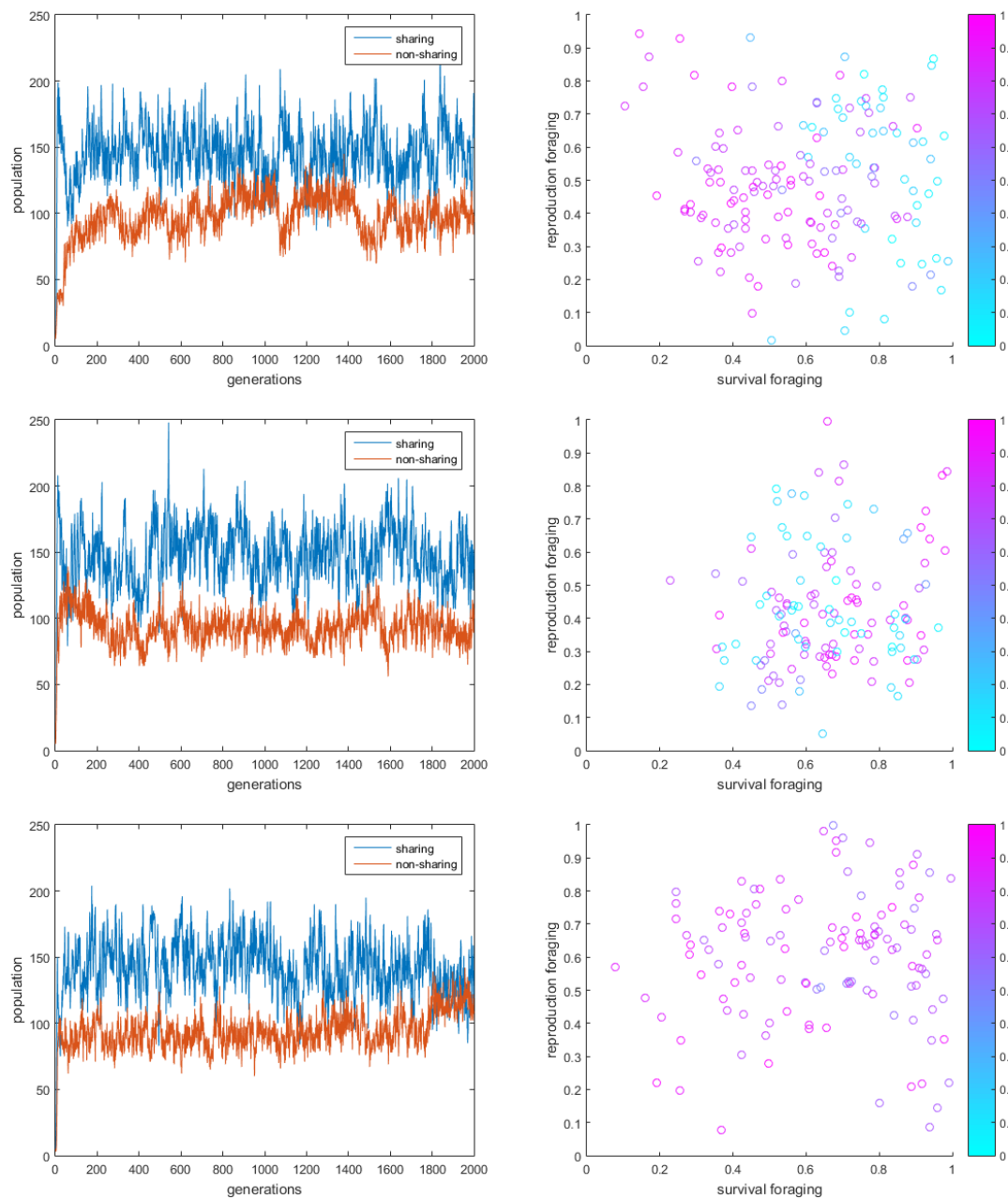


Figure 4.11 Sample runs of the two-resource model at 3 turns, $\mu = 0.09$.

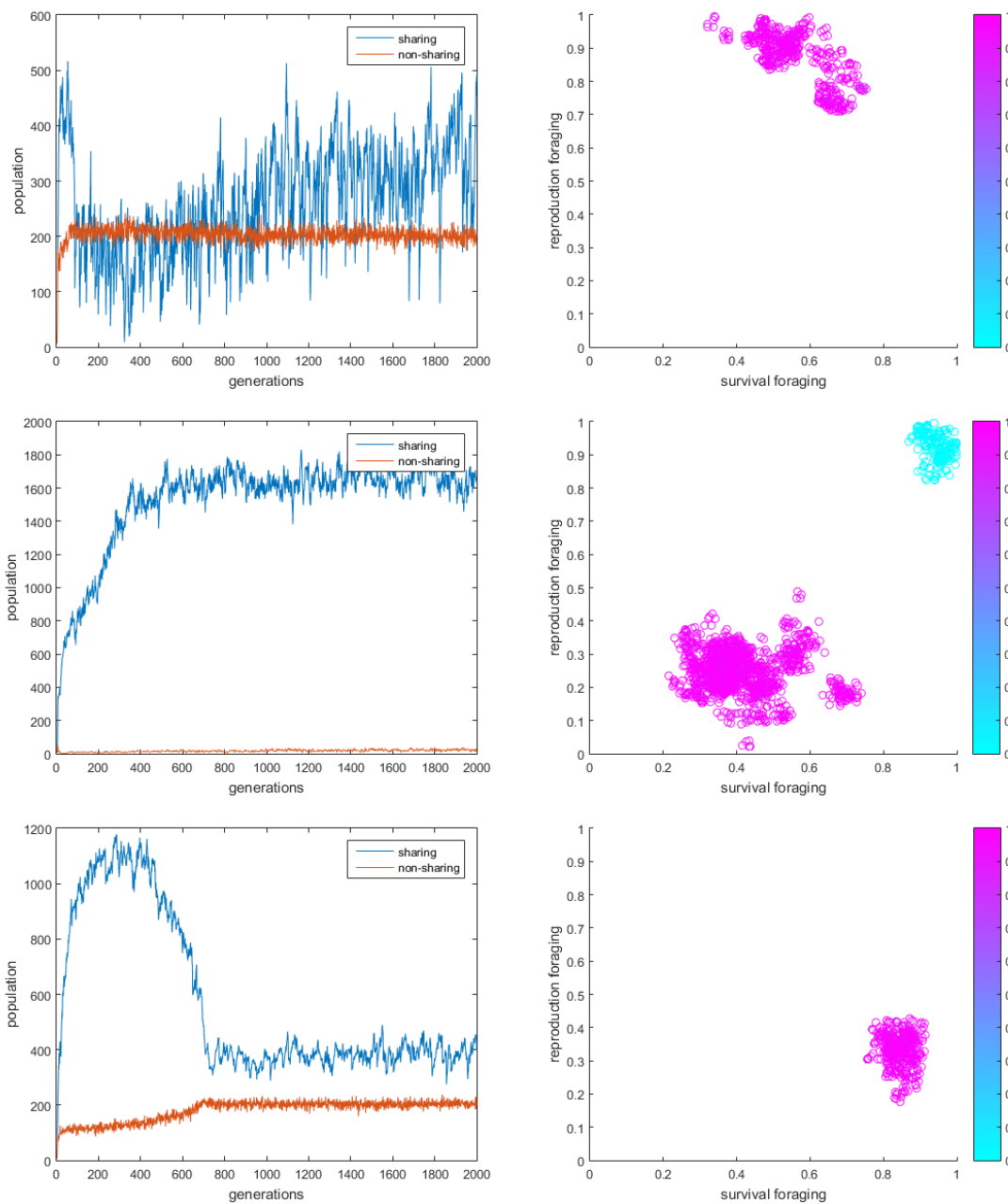


Figure 4.12 Sample runs of the two-resource model at 4 turns, $\mu = 0.01$.

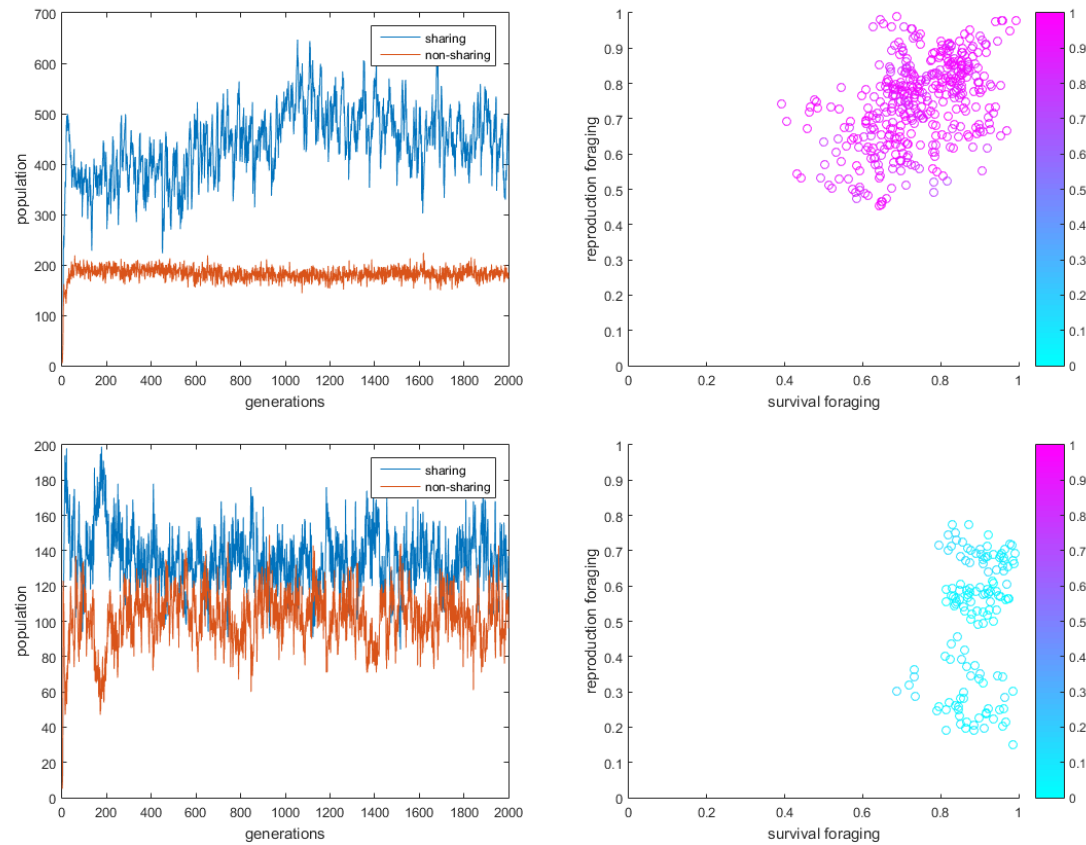


Figure 4.13 Sample runs at 4 turns, $\mu = 0.03$.

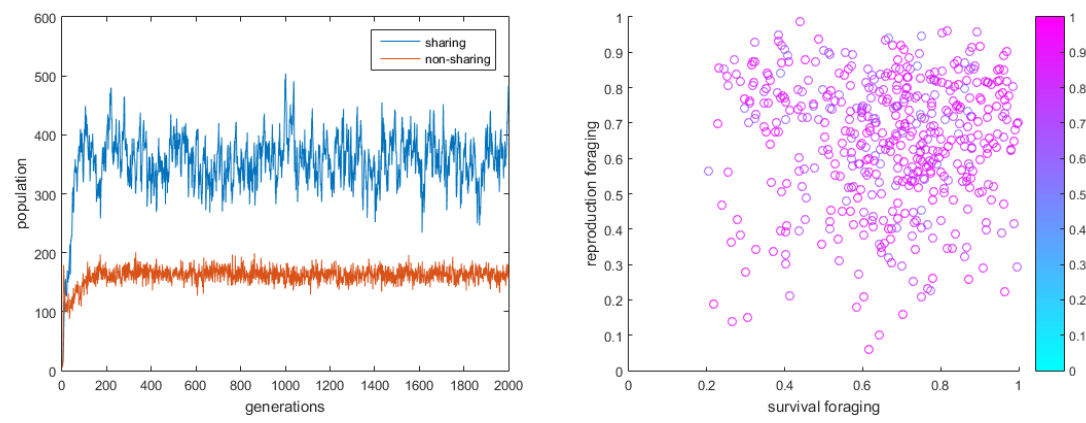


Figure 4.14 Sample runs at 4 turns and $\mu = 0.09$.

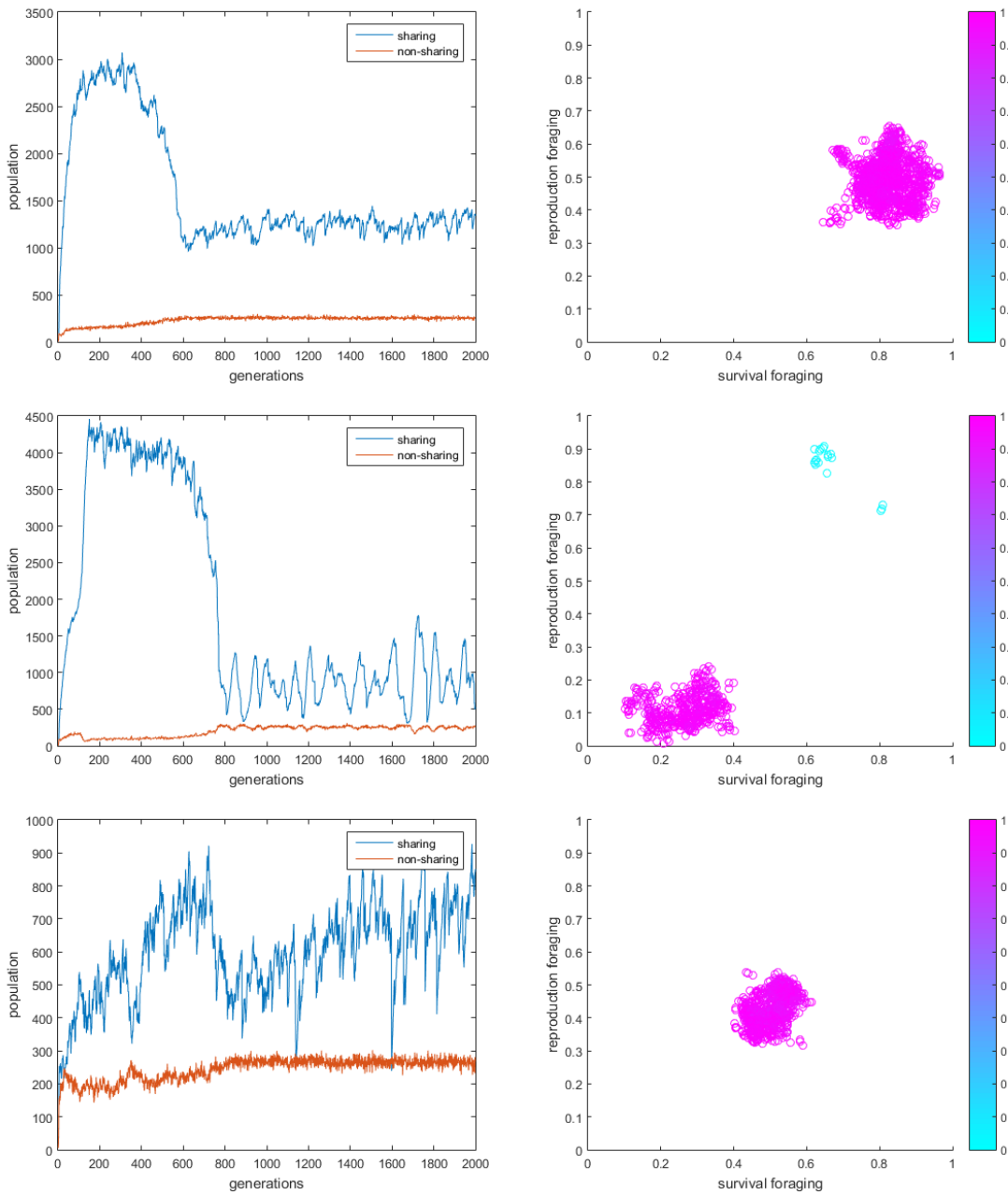


Figure 4.15 Sample runs at 5 turns, $\mu = 0.01$

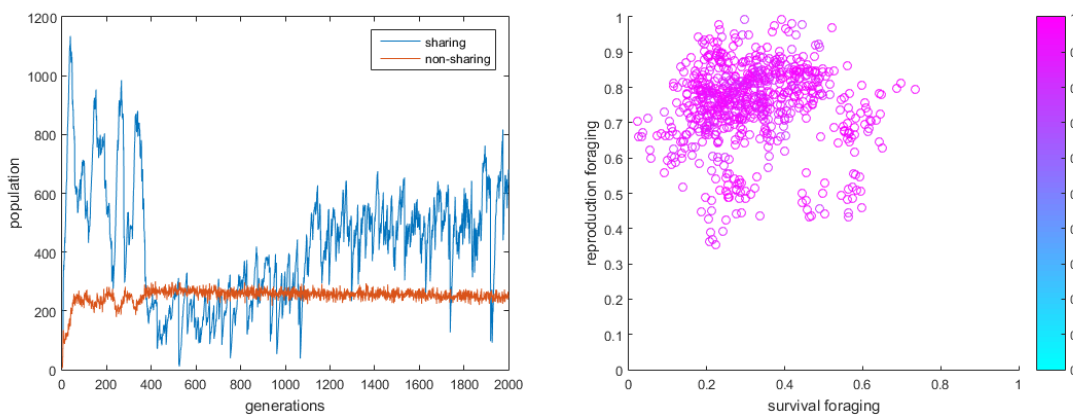
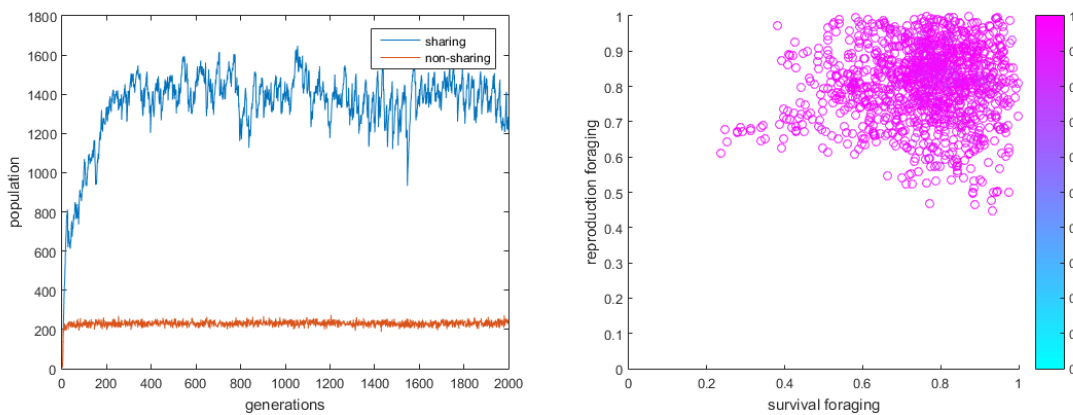


Figure 4.16 Sample runs at 5 turns, $\mu = 0.03$.

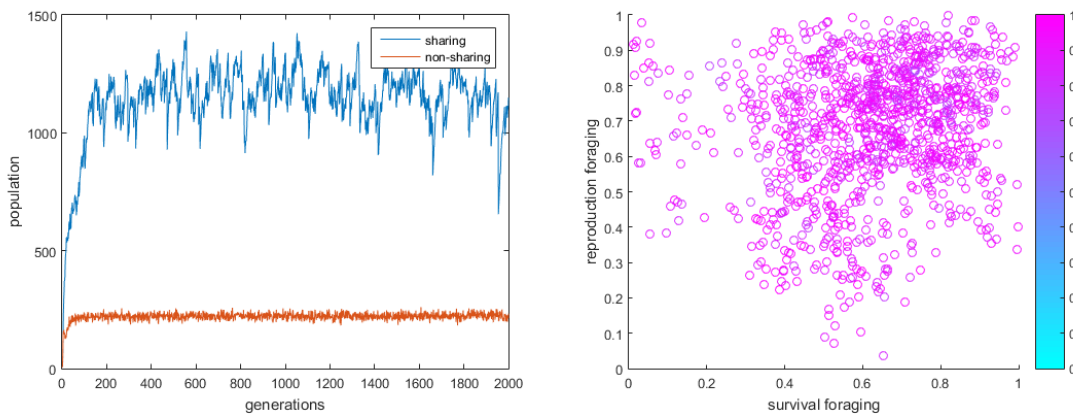


Figure 4.17 Sample runs at 5 turns and $\mu = 0.05$. Higher μ values had the same behavior.

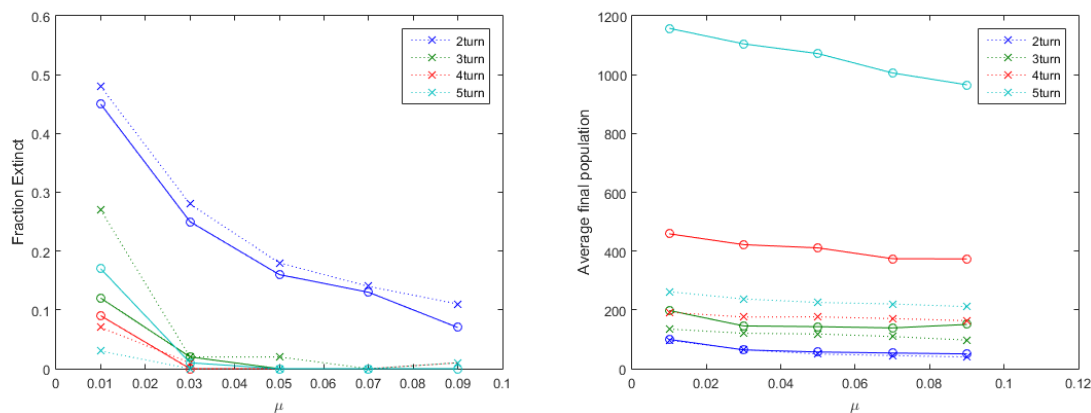


Figure 4.18 Extinction rate (left) and average final population (right) vs. μ for 2 resources. No foraging risk. Sharing group is solid lines (o), and non-sharing is dotted lines (x).

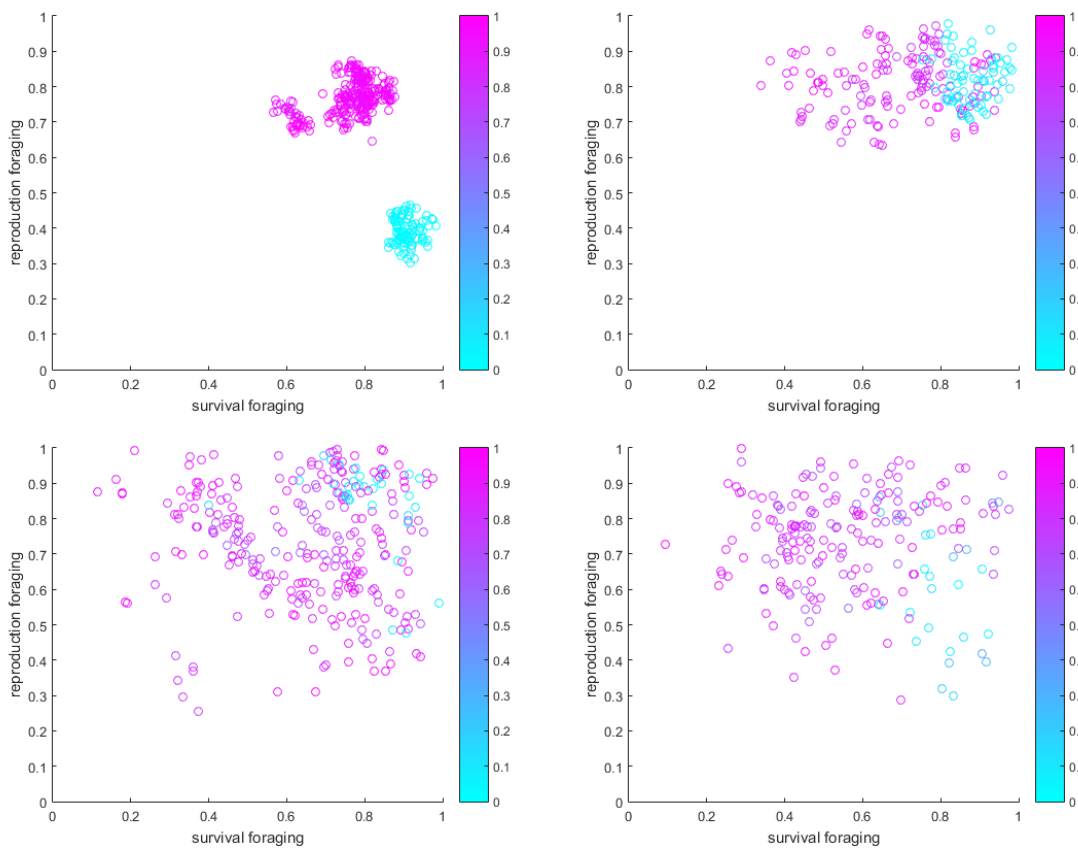


Figure 4.19 Bimodal distributions of social traits in two-resource model. $p = 0.01$ (top left), 0.03 in others, and $\mu = 0.01$ (top left), 0.03 (top right), 0.05 (bottom left) and $\mu = 0.07$ (bottom right).

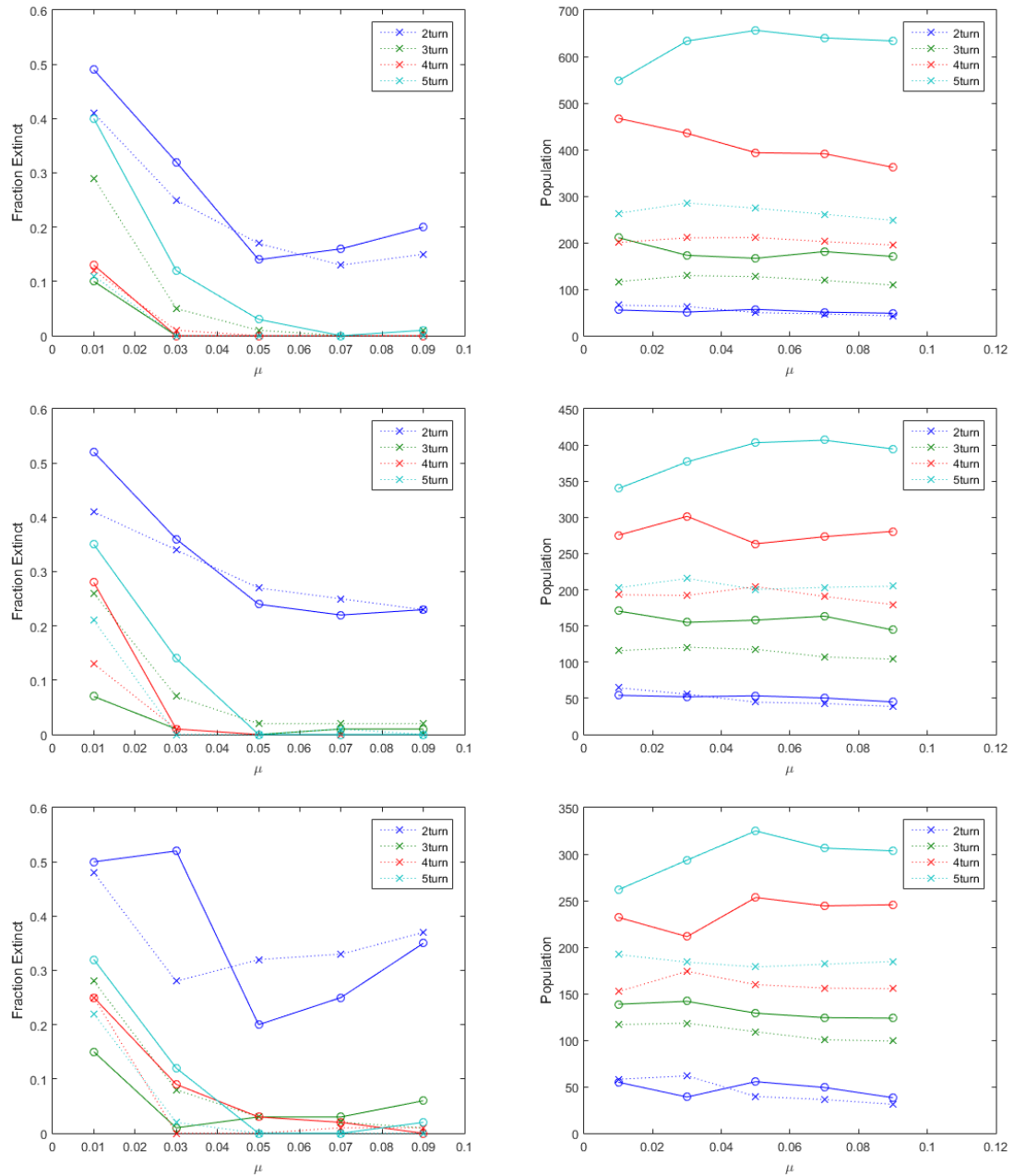


Figure 4.20 Extinction rates (left) and average final populations (right). Top to bottom, $p = 0.01, 0.03, \text{ and } 0.05$.

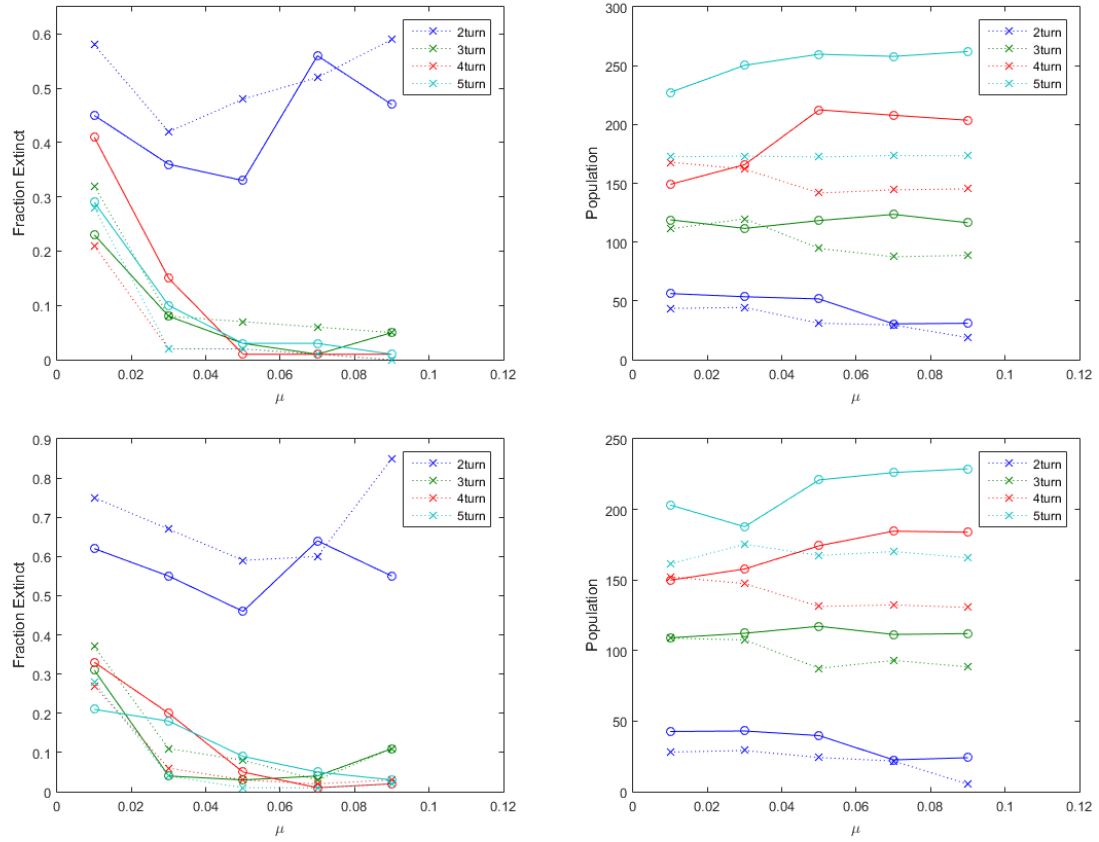


Figure 4.21 Extinction rates (left) and average final populations (right) at $p = 0.07$ and 0.09 . Top has $p = 0.07$, bottom has $p = 0.09$

5. DIVISION OF LABOR

This work has so far examined the effect of different trait distributions on the competition between the sharing and non-sharing groups, but it remains to be seen whether any of the presented phenotypic distributions are sufficient to demonstrate a quantifiable division of labor.

5.1. NORMALIZED MUTUAL ENTROPY

As mentioned in Section 2.4.1, the normalized mutual entropy (NME) in this model depends only on the trait values among the population, the population size, and the amount of resources. Due to the task probabilities having a dependence on resources, the most accurate measure of division of labor in this model occurs when resources are abundant. This is because even agents with low social traits are more likely to socialize than to forage when resources are depleted. The maximum amount of available resource in any one turn is 100 units, therefore only NME values for 100 units of resource are considered here.

5.1.1. Normalized Mutual Entropy for the Single-Resource Model. A population which only contains agents which have high foraging and low social traits represents the lowest NME values within the constraints of the model (Figure 5.1). Similarly, a population with only low foraging and high social traits has roughly the same NME value (Figure 5.2). A larger μ value increases the amount of variation in these same distributions, and also increases the value of NME (Figure 5.3). A distribution which is bimodal in the social trait has a value of NME which is roughly an order of magnitude larger than other distributions (Figure 5.4 left), but if the distribution is closer to uniform in the social trait than it is bimodal, then the value of NME is not much different from the case where distributions are biased towards one trait (Figure 5.4 right).

This result indicates that bimodality of the social trait is more important for the occurrence of division of labor in this model than is a range of trait values. Knowing this, one could assume that bimodality in both traits would produce a larger value of

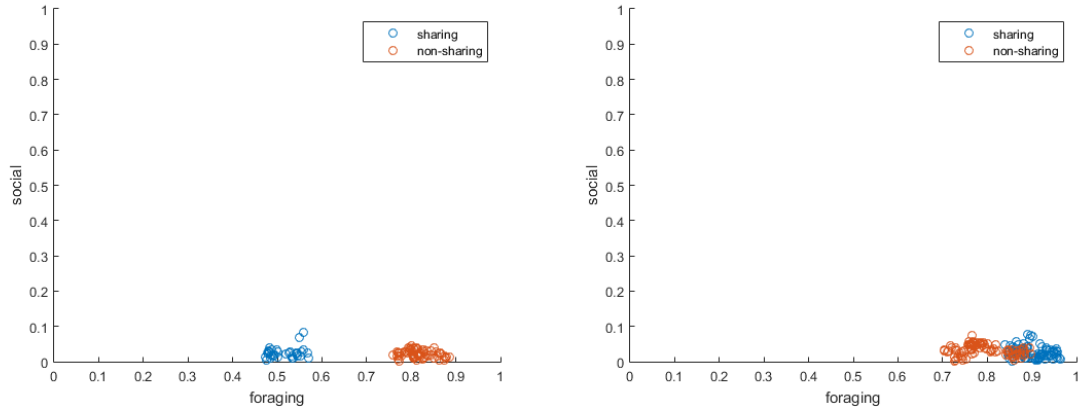


Figure 5.1 NME for the sharing group at low social, high foraging traits. Left has NME = 0.0006. Right has NME = 0.0010. For both figures, $\mu = 0.01$.

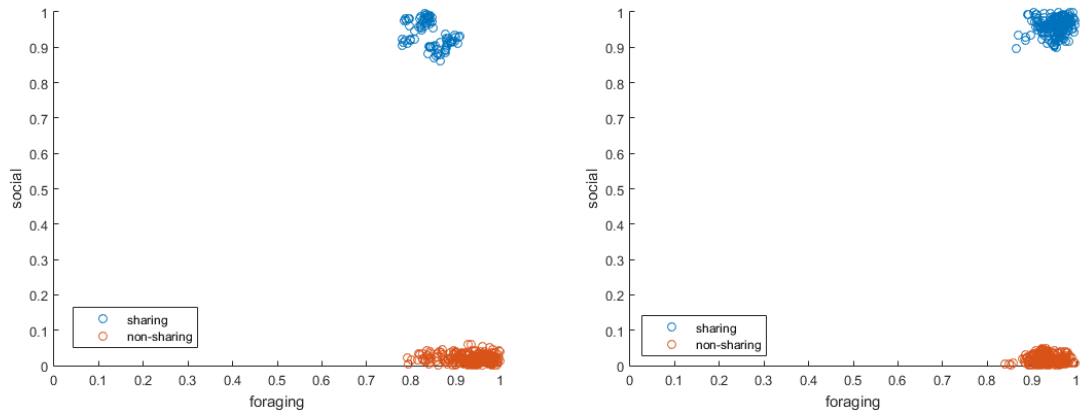


Figure 5.2 NME for the sharing group at low foraging, high social traits. Left has NME = 0.0015. Right has NME = 0.0009. For both figures, $\mu = 0.01$.

NME, and Figure 5.5 indicates that this is so, with the highest value of NME in the single resource model occurring when the distribution is bimodal in both traits.

While these sample figures give an indication to how trait distributions and system parameters affect NME, they are not perfectly sufficient to describe the importance of trait distribution when measuring division of labor. Figure 5.6 shows that NME is strongly correlated with the variance of the social trait and total variance among both traits, but that variance of the foraging trait is considerably less correlated with NME.

5.1.2. Normalized Mutual Entropy for the Two-Resource Model. The addition of a third trait, corresponding to an extra possible task, changes the range of values for NME.

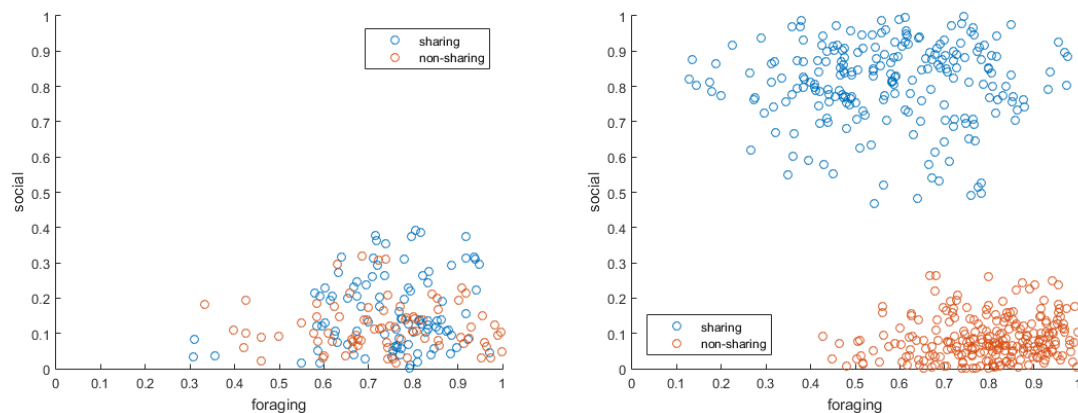


Figure 5.3 NME for sharing group when $\mu = 0.09$. Left has NME = .0080. Right has NME = .0082.

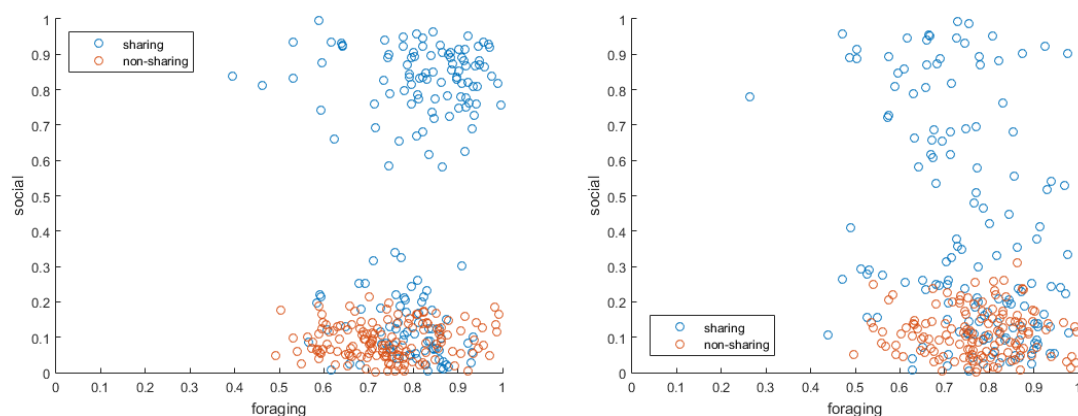


Figure 5.4 Trait plots for bimodal social trait. Left has NME = .0391 for $\mu = 0.07$. Right has NME = .0065 at $\mu = 0.09$.

Figure 5.7 shows that NME is again low for low social, low reproductive foraging, and high survival foraging, though it is an order of magnitude higher when there is greater variation in trait values. When the social trait is high (Figure 5.8), NME takes a range of values which again depends on the amount of variation in the population. The more tightly clustered the trait values, the lower the value of the normalized mutual entropy. When the social trait is bimodal (Figure 5.9), NME takes the largest values overall. As in the single resource model, NME is correlated with the social trait in the two-resource model, albeit less strongly. However, NME is now actually negatively correlated with foraging traits in the two-resource model (Figure 5.10).

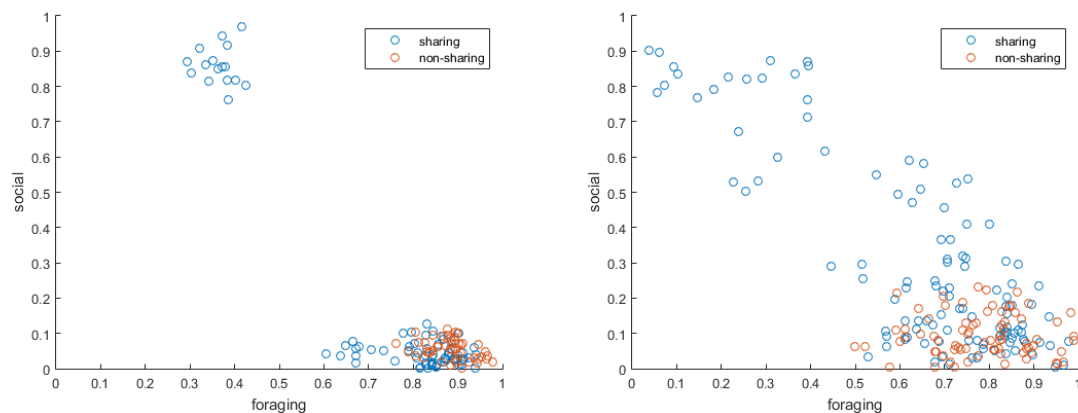


Figure 5.5 Trait plots which are bimodal in both traits. Left has $\mu = 0.03$, and NME = 0.0520. Right has $\mu = 0.07$, and NME = 0.0475.

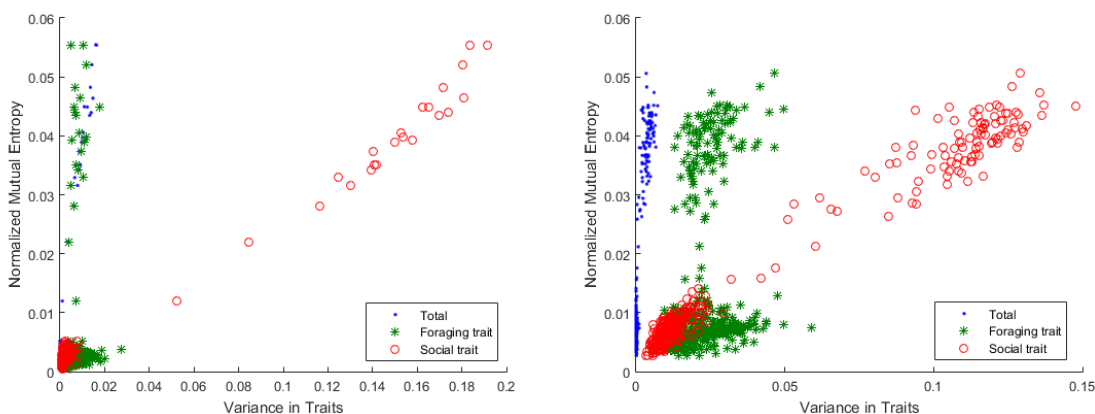


Figure 5.6 NME – trait variance correlation plots in single resource model. Left panel ($\mu = 0.03$) has correlation coefficient $R = 0.1319$ for foraging trait, 0.9939 for social trait, and 0.9896 for both traits together. Right panel ($\mu = 0.09$) has $R = 0.2123$ for foraging trait, 0.9877 for social trait, and 0.9254 for both traits. Data is from sharing group only, from all parameter values.

5.2. FRACTION FORAGERS

The quantity “fraction foragers” in this work is defined as the total number of foragers in a generation divided by the population size. Therefore, this quantity will be a maximum if all agents forage at every opportunity during a generation, and the maximum value is equal to the number of turns per generation. Only data from the sharing population in the single-resource model is presented here. It was established in Chapter 3 that large fluctuations in the sharing group’s population size occurred when there were agents with high social trait values. Here it is shown that larger fluctuations in the

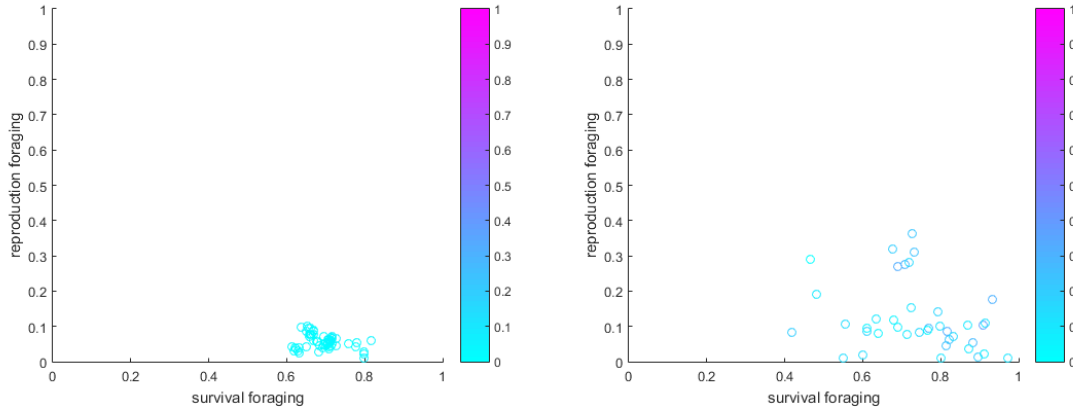


Figure 5.7 Trait plots with high survival foraging and low social traits. Left has $\mu = 0.01$, and NME = 0.0019. Right has $\mu = 0.09$, and NME = 0.0135.

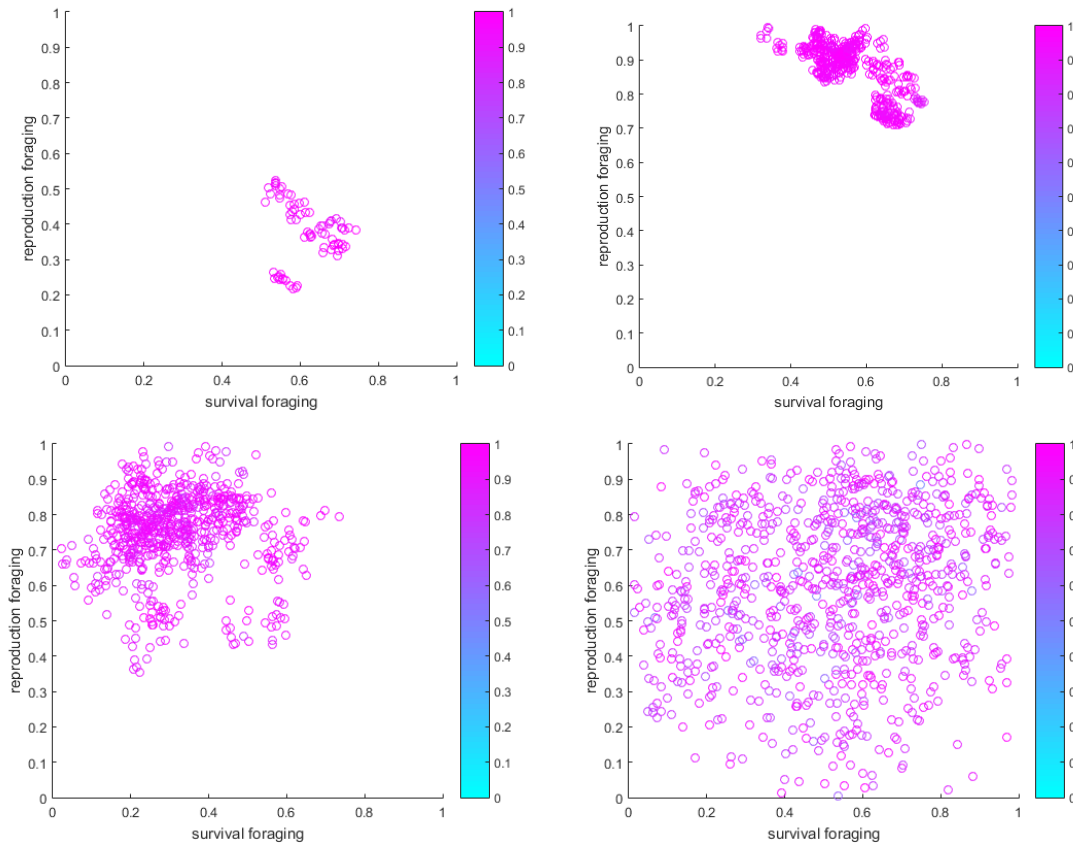


Figure 5.8 Trait plots in two-resource model with high social traits. Top row are $\mu = 0.01$ with NME = 0.0022 (top left), and 0.0011 (top right). Bottom left is $\mu = 0.03$ with NME = 0.0028 (bottom left). Bottom right is $\mu = 0.09$ with NME = 0.0060.

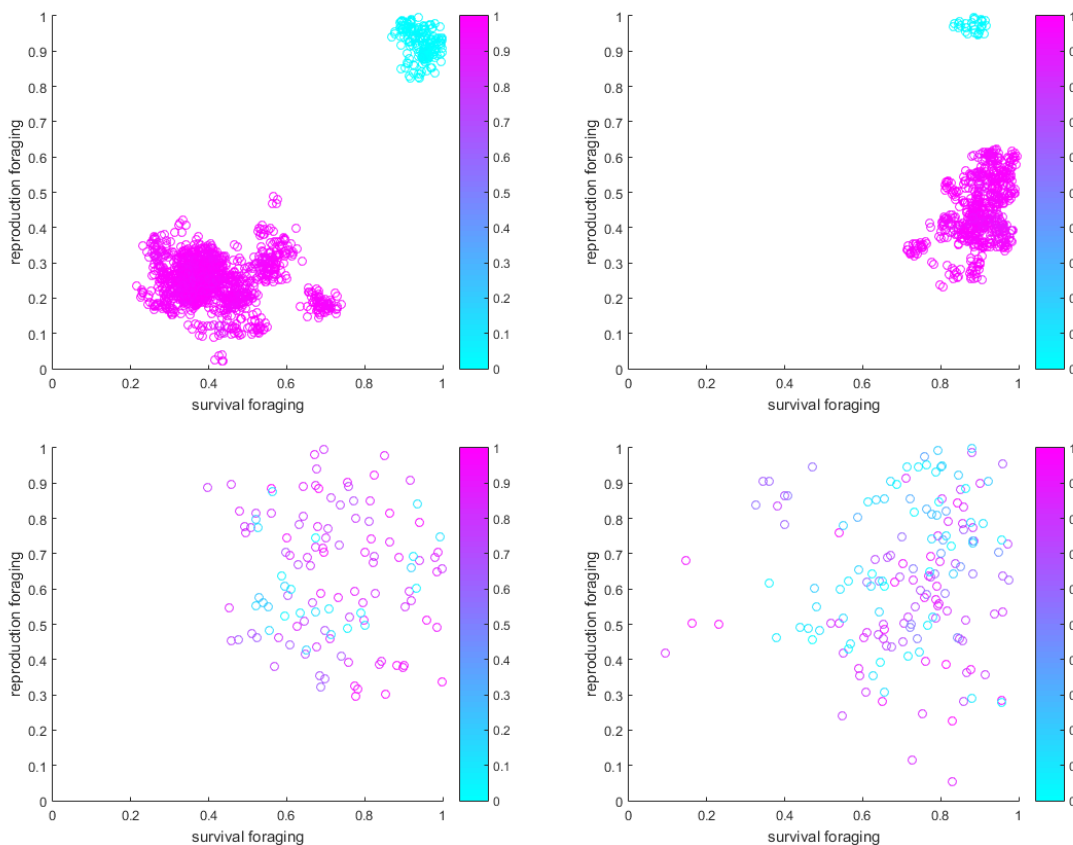


Figure 5.9 Trait plots with bimodal distributions in the social trait. Top row has $\mu = 0.01$, and (left to right) $NME = 0.0366$ and 0.0127 . Bottom row has $\mu = 0.07$ (left) and 0.09 (right), with $NME = 0.0203$ and 0.0316 , respectively.

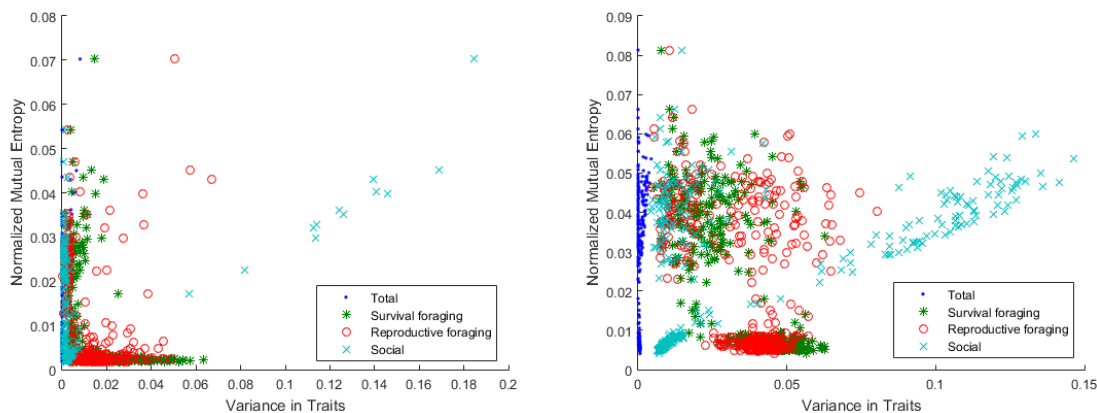


Figure 5.10 NME - trait variance correlation plots for two-resource model. Left panel ($\mu = 0.03$) has correlation coefficient $R = -0.4325$ for the survival foraging trait, -0.1964 for the reproductive foraging trait, 0.4978 for the social trait, and 0.4418 total. Right panel ($\mu = 0.09$) has correlation coefficient $R = -0.7494$ for the survival foraging trait, -0.4110 for the reproductive foraging trait, 0.5639 for the social trait, and 0.3217 for the total variance.

population size correspond to erratic behavior in fraction foragers (Figure 5.11), and that erratic behavior in fraction foragers also corresponds to the presence of social traits (Figure 5.12).

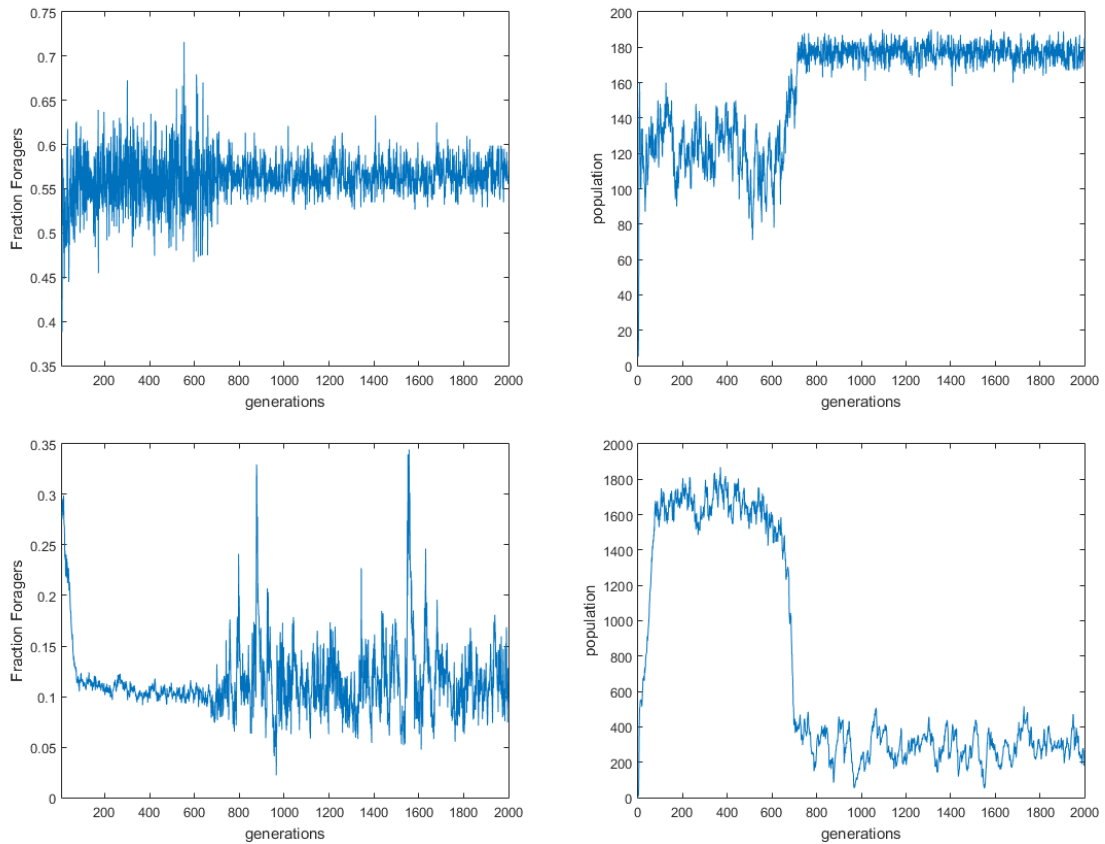


Figure 5.11 Fraction foragers predicts population fluctuations. Left is fraction foragers vs. time, right is population vs. time. Parameters are $\mu = 0.05$, 2 turns (top row), and $\mu = 0.01$, 4 turns (bottom row)

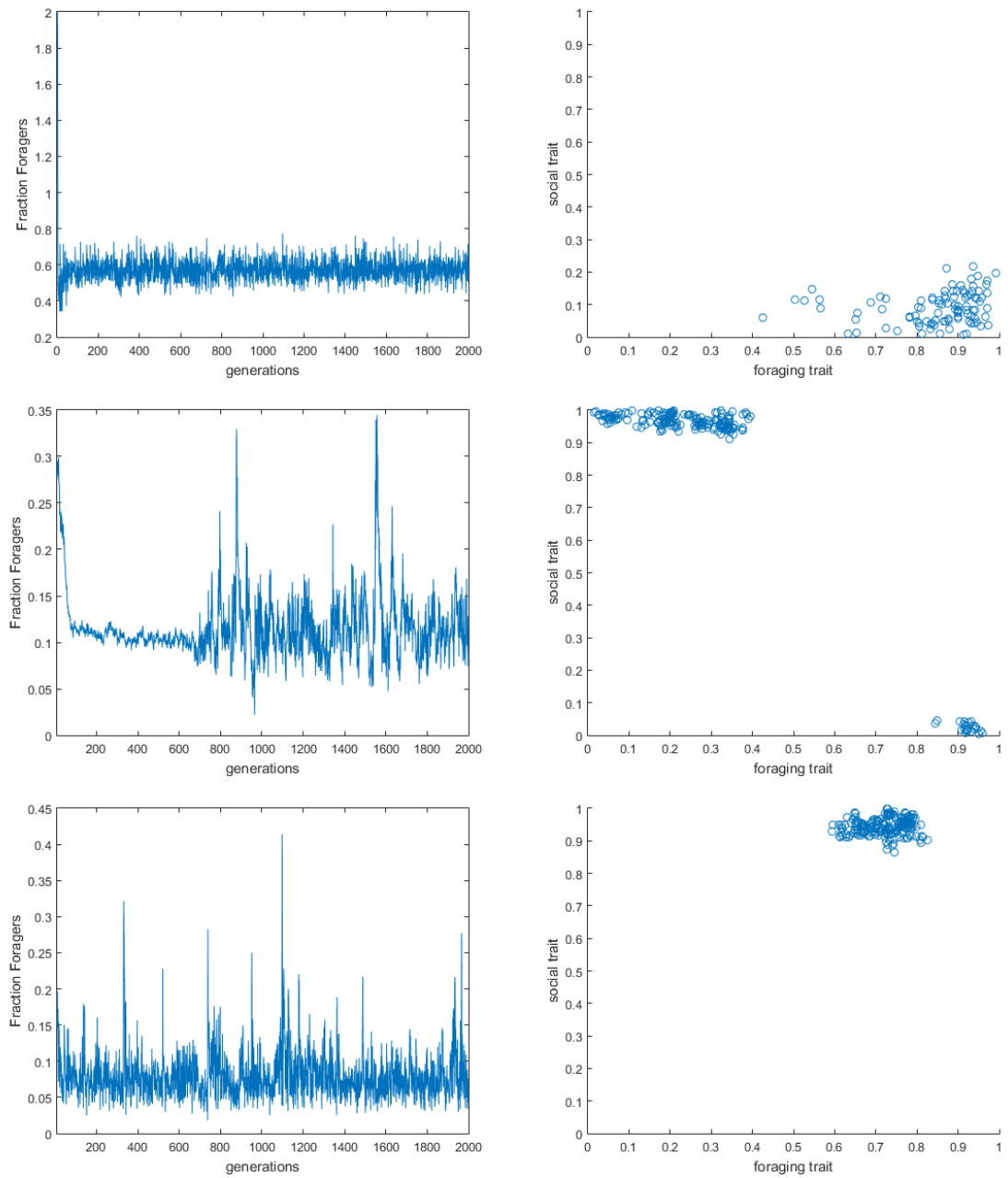


Figure 5.12 Erratic behavior in fraction foragers occurs when sharing group has social traits. Left column is fraction foragers vs. time, right column is trait plots at the 2000th generation. Parameters are $\mu = 0.05$, 2 turns (top row), and $\mu = 0.01$, 4 turns (middle and bottom rows)

6. CONCLUSIONS

6.1. DISCUSSION

The model presented in this work contains elements of both group selection and kin selection. The competition between the two groups represents group selection, but the fact that agents in the sharing group can only share with other cooperating agents is kin selection, particularly when the population has similar trait values as these values most likely came from a single parent.

It is seen that this cooperative sharing behavior can cause a fitness advantage relative to the group which does not share resources, and even when the sharing group has a disadvantage due to the social trait, the population remains quite stable, persisting for thousands of generations. This emphasizes a point which is often ignored when discussing evolution, which is that any trait which is not driven to extinction can exist. The idea that all traits observed in nature are due to some advantage provided to the organism is simple and reasonable. However this work shows that traits which may not result in a fitness advantage to the organism can still exist under the right circumstances, though the model is limited in the ability to test this hypothesis further.

This model was created to develop division of labor without task-switching costs. Depending on how strictly one defines division of labor, this is both true and false. The model can produce agents which specialize on a specific task, but it is not capable of producing agents which never engage in a specific task. It may still be true that evolving organisms which do not reproduce, or which lose the ability to do some task, requires task-switching costs, but this model was focused on phenotypic specialization.

6.2. FUTURE WORK

The basic details and behavior of the model have been laid out, but there are many questions that are left unanswered, which future work could examine. Some data already exists to answer these questions, and other questions are extensions of the model which would have required far too much time to explore in one dissertation. One of the largest undertakings would be to run thousands of simulations of versions with the foraging risk

to eliminate the variance in the results for the extinction rates, and implementing a risk on the survival resource, or both resources.

From a biological perspective, there are some adjustments to the model that would perhaps be more realistic. For example, beginning simulations with traits uniformly randomly distributed is unnatural. If the ability to share resulted from a mutation in a previous generation, the offspring of the organism carrying such a mutation would have traits similar to the parent, and not be distributed uniformly. The initial populations should be distributed in a manner so that the agents are closer to a central peak, the peak representing the parent's traits. A good first attempt would probably be a normal distribution with standard deviation μ , and then also distributing offspring in the model with a normal distribution as opposed to just being a box of height and width 2μ . Thus the parameter μ would not control the maximum amount of variation, but the typical amount. The location of the peak would also be a parameter, and it may be that a certain combination of peak location and mutability would tend to lead to one distribution, while another combination of these parameters could lead to a different distribution.

Cheating is a major question that this model has not addressed, as it assumed that agents in one group did not directly interact with members of the other group. A simple method to explore the effect of cheating in this model is to allow mixing between the two groups, i.e., that agents can socialize (and therefore share resources) with agents belonging to the other group. This may produce agents in the non-sharing group who evolve high social traits, as a secondary method of acquiring resources. Or it may cause the sharing group to simply go extinct more often. The code for allowing mixing is already written, but no simulations were run to test this type of cheating behavior.

On the topic of extinctions, it is possible that the small initial populations had a significant effect on the rates of extinction, particularly since the times to extinction were very short. Performing additional simulations with larger initial populations could be serve to test this hypothesis. A related set of simulations could test whether the relative sizes of the initial populations affect extinction, e.g., if the sharing group begins with half of the size of the non-sharing group. Part of this work included an incomplete dataset to

explore this question, though these datasets are unanalyzed. This work will be included in a future paper.

Further analysis of the results presented here are also underway and to be included in a future paper. This includes tracking the stability of social clusters over time, and mapping all simulations at each parameter set onto a single figure to more clearly identify the fitness peaks in trait space.

**APPENDIX:
MATLAB CODE**

```

%% Initialization

N0 = 5; % Initial population
agents1 = unifrnd(0,1,2,N0); % 2xN vector of trait values on (0,1)
agents2 = unifrnd(0,1,2,N0);
turns_per_gen = 2;

R0 = 10; % Initial resource amount
R = R0;
R_in = 100; % Resource influx(constant flow), or max(logistic growth)
mu1 = .01; % Allowed deviation of offspring from parents
mu2 = mu1;
w0 = 2; % Neutral fitness value
time_stop = 2000; % Number of generations
BigJ = 0; % Selection toggle

food_thresh = 0; % Survival threshold

pop_size1 = zeros(1,time_stop);
pop_size2 = zeros(1,time_stop);
trait_gens1 = cell(1,time_stop); % trait data storage
trait_gens2 = cell(1,time_stop);
parent1 = nan(1,time_stop);
parent2 = nan(1,time_stop);

pop_size1(1) = N0;
pop_size2(1) = 0;
trait_gens1(1) = mat2cell(agents1(1:2,:), [2]);
trait_gens2(1) = mat2cell(agents2(1:2,:), [2]);
dead1 = 0; % tracking possible extinctions
dead2 = 0;

agents1(3,:) = zeros(1,N0);
agents2(3,:) = zeros(1,N0);

foragers1 = zeros(turns_per_gen,time_stop);
foragers2 = foragers1;

%% Section II - Main

% Assuming there are 2 possible types of particles (agents and resources)
% with agents in 2 possible states (food or no food), then probability that

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% an agent forages p_f ~ R, probability that he socializes p_s ~ N-1.
% Socializing then produces 2 outcomes, depending on whether he finds an
% agent with food or without. After that step is done, agents who have
% food will reproduce with probability r.

for t = 2:time_stop

    % TURNS
    for turn = 1:turns_per_gen
        if R < 0
            R = 0;
        end
        % logistic equation resource growth
        dR = 2*R0*(1-(R0/R_in));
        R = R + dR;    % Increment resource
        R0 = R;       % Store resource to determine growth between turns

        % Get population sizes
        N1 = size(agents1,2);
        N2 = size(agents2,2);
        % Forage/sharing loop
        reorder = choozrand(1:N1+N2,N1+N2); % choozrand reorders any 1xN vector
        % indices from 1:N1 are agents1, N1+1:N1+N2 are agents2

        for j = 1:N1+N2
            if reorder(j) < N1+1
                T = [R+1 N1-1];
                p_f = agents1(1,reorder(j))*(R+1)/(T*agents1(1:2,reorder(j)));
                roll = unifrnd(0,1);
                if roll < p_f    % forage
                    if (R > 0)
                        R = R-1;
                        agents1(3,reorder(j)) = agents1(3,reorder(j)) + 1;
                        foragers1(turn,t) = foragers1(turn,t) + 1;
                    end
                else roll = unifrnd(0,1);
                    if roll < agents1(2,reorder(j))
                        % share
                        tosser = [1:reorder(j)-1,reorder(j)+1:N1];
                        pick = choozrand(tosser,1);
                        agents1(3,reorder(j)) = (agents1(3,reorder(j)) + agents1(3,pick))/2;
                        agents1(3,pick) = agents1(3,reorder(j));
                    end
                end
            else T = [R+1 N2-1];
                index = reorder(j)-N1;

```



```

    p_f = agents2(1,index)*(R+1)/(T*agents2(1:2,index));
    roll = unifrnd(0,1);
    if roll < p_f
        if (R > 0)
            R = R-1;
            agents2(3,index) = agents2(3,index) + 1;
            foragers2(turn,t) = foragers2(turn,t) + 1;
        end
    end
end
end
end

end

% Reproduction loop
next_agent = nan(2,1);
newegg = [];
if isempty(agents1) == 0
    n_A1 = find(agents1(3,:) > food_thresh);
    r1 = agents1(3,n_A1);
    kk = 1;
    w1 = floor(r1) + w0; % Setting fitness values

    for k = 1:length(n_A1)
        roll = unifrnd(0,1);
        % reproduction1
        if r1(k) > 1
            if roll < (r1(k) - floor(r1(k)))
                newegg = braket_reproduction(agents1(1:2,n_A1(k)),w1(k),mu1);
                kids = w1(k);
            else
                newegg = braket_reproduction(agents1(1:2,n_A1(k)),w1(k) - 1,mu1);
                kids = w1(k) - 1;
            end
        elseif roll < r1(k)
            newegg = braket_reproduction(agents1(1:2,n_A1(k)),w0,mu1);
            kids = w0;
        end
        if isempty(newegg) == 0
            cut1 = find(newegg>1 | newegg<0);
            % boundary death
            if isempty(cut1)
                next_agent(1:2,kk:kk+kids-1) = newegg;
                parent1(kk:kk+kids-1,t) = n_A1(k);
                kk = kk+kids;
            else for b = 1:size(newegg,2)

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```

        c = find(newegg(:,b)>1 | newegg(:,b)<0);
        if isempty(c)
            next_agent(1:2,kk) = newegg(:,b);
            parent1(kk,t) = n_A1(k);
            kk = kk+1;
        end
    end
end
else next_agent(1:2,kk) = agents1(1:2,n_A1(k));
    parent1(kk,t) = 0;
    kk = kk+1;
end
clear kids;
newegg = [];
end

end

% extinction check 1
if isempty(find(isnan(next_agent),1))
    new_N = size(next_agent,2);
    next_agent(3,:) = zeros(1,new_N);
    agents1 = next_agent;
    pop_size1(t) = new_N;
    trait_gens1(t) = mat2cell(agents1(1:2,:), [2]);
elseif dead1 == 0
    fprintf('population 1 is extinct at generation %g. \n',t);
    agents1 = [];
    dead1 = t;
end
next_agent = nan(2,1);

if isempty(agents2) == 0
    n_A2 = find(agents2(3,:) > food_thresh);
    r2 = agents2(3,n_A2);
    jj=1;
    w2 = floor(r2) + w0; % fitness values
    for k = 1:length(n_A2)
        roll = unifrnd(0,1);
        % reproduction2
        if r2(k) > 1
            if roll < (r2(k) - floor(r2(k)))
                newegg = braket_reproduction(agents2(1:2,n_A2(k)),w2(k),mu2);
                kids = w2(k);
            else newegg = braket_reproduction(agents2(1:2,n_A2(k)),w2(k) - 1,mu2);
                kids = w2(k) - 1;
            end
        end
    end
end

```

```

        end
    elseif roll < r2(k)
        newegg = braket_reproduction(agents2(1:2,n_A2(k)),w0,mu2);
        kids = w0;
    end
    if isempty(newegg) == 0
        cut2 = find(newegg>1 | newegg<0);
        if isempty(cut2)
            next_agent(1:2,jj:jj+kids-1) = newegg;
            parent2(jj:jj+kids-1,t) = n_A2(k);
            jj = jj+kids;
        else for b = 1:size(newegg,2)
            c = find(newegg(:,b)>1 | newegg(:,b)<0);
            if isempty(c)
                next_agent(1:2,jj) = newegg(:,b);
                parent2(jj,t) = n_A2(k);
                jj = jj+1;
            end
        end
    end
    else next_agent(1:2,jj) = agents2(1:2,n_A2(k));
        parent2(jj,t) = 0;
        jj = jj+1;
    end
    clear kids;
    newegg = [];
end

end
% extinction check
if isempty(find(isnan(next_agent),1))
    new_N = size(next_agent,2);
    next_agent(3,:) = zeros(1,new_N);
    agents2 = next_agent;
    pop_size2(t) = new_N;
    trait_gens2(t) = mat2cell(agents2(1:2,:), [2]);
elseif dead2 == 0
    fprintf('population 2 is extinct at generation %g. \n',t)
    agents2 = [];
    dead2 = t;
end
% clear update vector
clear next_agent;
end

```

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