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# EVOLUTIONARY GAME THEORY AND POPULATION GENETICS

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## 1 Introduction

This project explores a proposed analogy between methods used in Evolutionary Game Theory to predict changes in individual players' choices over each round of play based on expected reward/payoff, and standard models for the genetic dynamics of a population reproducing under sexual selection. The Methods used in this project are essentially a replication of the algorithms given in *Chastain et al.* However, the Discussion section will include evaluations of these methods, including claims from outside literature which bring into question the assertions made in *Chastain et al.*

## 2 Background

This section will give relevant definitions from Game Theory, and state the assumptions of the model from theoretical population genetics to which the game-theoretic model is compared.

### 2.1 Biological Assumptions

The population genetic model used here assumes an infinite, panmictic population of haplotypes reproducing under weak sexual selection, chosen here to be  $s = 0.01$ . The population is described in terms of genotype frequencies, which result from the consideration of two loci under infinite recombination, effectively selecting alleles independently at each locus. Weak sexual selection is the only evolutionary pressure considered here (effects such as genetic drift are thus ignored). A key concept used in the Population Genetics derivation relies on the assumption of constant zero linkage disequilibrium, the evolutionary process is then said to occur "on the Wright Manifold," where the linkage disequilibrium is zero (*Chastain et al.*, *Meir and Parkes*).

### 2.2 Relevant Concepts from Game Theory

A game is a mathematical model of adversarial interactions between two or more agents, called players. Each player has a set of actions available to them, each element of which is called a *pure strategy*. A game is typically described in *normal form* via a payoff matrix (or pair of matrices, one for each player). This matrix encodes the values of the payoff function for each pair of player strategies. The payoff/utility function will be discussed in more detail in the following section.

**Coordination Games** The specific type of game studied here as an analogy for genetic evolution under selection is a *coordination game*. This is defined as a game in which the utility function is the same for all players (*Chastain et al.*, *Meir and Parkes*). A *zero-sum* game is one in which the payoff to one player for each strategy is of same magnitude and opposite algebraic sign as that to the other. That is, the net gain or loss of utility is zero.

## 3 Methods

This section details the mathematical methods being implemented and compared in this project. Algorithms will be presented as used, in addition to some outside theoretical considerations for context and comparison.

### 3.1 Mathematical Formulations of Evolutionary Game Theory Approach

In a game involving  $n$  players each player  $i$  has a pure strategy space  $S_i$ , the set of all actions available to them. In this case, 3 allele actions are available to each locus player, denoted  $A$  and  $B$ , with pure allele strategy spaces

$S_A = \{A1, A2, A3\}$  and  $S_B = \{B1, B2, B3\}$ . The payoff function for the game  $u_i$  is given by  $u_i : \times_{i \in \{A,B\}} S_i \mapsto \mathbb{R}$ , where the domain is the product space of the pure strategy spaces, and gives all possible strategy combinations, i.e.  $\{(A1,B1),(A1,B2),...,(A3,B3)\}$ . The payoffs are encoded in payoff matrices  $Q$ . The payoff matrix is defined as:

$$Q_{col} = \begin{bmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{bmatrix} \quad (1)$$

In the above matrix,  $q_{ij}$  is the payoff when one player plays strategy  $i$  and the other plays strategy  $j$ . Since the games considered here are zero-sum, and by convention the payoff matrix implicitly represents the column player, the row player's payoff matrix is given by:

$$Q_{row} = \begin{bmatrix} -q_{11} & -q_{12} & -q_{13} \\ -q_{21} & -q_{22} & -q_{23} \\ -q_{31} & -q_{32} & -q_{33} \end{bmatrix} \quad (2)$$

**Multiplicative Weight Update Algorithm (MWUA)** The mixed strategy profiles for each player are row or column vectors containing probabilities assigned to each possible action, as over repeated rounds of play, players may choose to play each action with certain probability instead of always choosing the same action. In this implementation, the mixed

strategy profile for locus  $A$  is the column vector  $\begin{bmatrix} a_1 \\ a_2 \\ a_3 \end{bmatrix}$  and the mixed strategy profile for locus  $B$  is the row vector  $[b_1 \ b_2 \ b_3]$  with each entry being the probability of the corresponding locus player choosing to play the allele given by the index. As given in *Chastain et al*, the Multiplicative Weight Update changes the mixed strategy profile for the next round of play according to the expected payoff of the strategy. Here the expected utility is that to locus  $A$  playing allele strategy  $i$  in the (polynomial weight) MWUA is

$$\bar{u}_i^t = \sum_{j \in S_A} y_j^t q_{ij} \quad (3)$$

where  $y_j^t$  is the probability of player  $B$  playing allele  $j$  given that locus  $A$  plays  $i$ . Derivation taken from *Meir and Parkes*, *Chastain et al*. See *Meir and Parkes* for fully detailed derivation. The MWUA update rule for the strategy  $i$  in mixed strategy profile  $a$  is

$$a_i^{t+1} = \frac{a_i^t (1 + \epsilon u_i^t)}{1 + \epsilon \sum_{k \in S_A} a_k u_k}$$

The above is for strategy  $i$  in the mixed strategy of locus player  $A$ , but holds for all strategies and locus player  $B$  as well. In this context, the parameter  $\epsilon$  is the selection strength  $s$ .

**Mixed Strategy Nash Equilibria** The mixed strategies  $\mathbf{a}, \mathbf{b}$  are a Nash equilibrium of a game with payoffs  $q_{ij}$  if

$$\forall i' \in S_A : \sum_{j \in S_B} b_j q_{i'j} \sum_i \sum_j a_i b_i q_{ij} \quad (4)$$

The same holds for all  $j' \in S_B$ . From *Meir and Parkes*.

### 3.2 Mathematical Formulation of Population Genetics Approach

As in *Chastain et al.*, the population genetic dynamics are represented in terms of two matrices. One matrix represents the frequencies of all possible genotypes at a specific (discrete) timestep. The other is a fitness matrix for each genotype, dictating how the genotype frequencies change across timesteps. As a departure from the notation in *Chastain et al.*, the fitness matrix is denoted  $F$ , the genotype frequency matrix  $G$ . In this implementation, each of 2 loci has 3 alleles, so both  $F$  and  $G$  are  $3 \times 3$  matrices. The population genetics dynamics were implemented as in the Supporting Information for *Chastain et al*.

$$F = \begin{bmatrix} f_{11} & f_{12} & f_{13} \\ f_{21} & f_{22} & f_{23} \\ f_{31} & f_{32} & f_{33} \end{bmatrix} \quad G = \begin{bmatrix} g_{11} & g_{12} & g_{13} \\ g_{21} & g_{22} & g_{23} \\ g_{31} & g_{32} & g_{33} \end{bmatrix}. \quad (5)$$

In the above matrices,  $f_{ij}$  denotes the fitness of genotype  $ij$ , with the each index representing the allele number at the respective locus. Likewise,  $g_{ij}$  is the frequency of the corresponding genotype.

The equation below gives the change in frequencies across each timestep, that is, the genotype update dynamics. Note that the fitness matrix is constant, as in the Supporting Information to *Chastain et al.*, but not necessarily in the original paper, since a time-dependency is introduced and later dropped without explanation. Most texts, including *Meir and Parkes* treat a constant fitness matrix as standard. Note that the sum in the denominator ensures that the genotype frequencies remain a probability distribution.

$$g_{ij}^{t+1} = \frac{g_{ij}^t f_{ij}}{\sum_{ij} g_{ij}^t f_{ij}} \quad (6)$$

## 4 Results

Simultaneous simulations of both the population genetic dynamics and MWUA for the coordination game were run using the values given in *Chastain et al.* in an attempt to reproduce the given sample output for illustrative purposes. As is explained in *Chastain et al.*, the fitness matrix  $F$  is defined in terms of the payoff matrix  $Q$  (or vice versa). They are related by  $q_{ij} = \frac{(f_{ij}-1)}{s}$ . The payoff and fitness matrices used in the simulation were

$$Q = \begin{bmatrix} 2 & 3 & -1 \\ 0 & 1 & -2 \\ 1 & 4 & 2 \end{bmatrix} \quad F = \begin{bmatrix} 1.02 & 1.03 & 0.99 \\ 1 & 1.01 & 0.98 \\ 1.01 & 1.04 & 1.02 \end{bmatrix} \quad (7)$$

The genotype frequencies were initialized such that all nine possible genotypes were of equal initial frequency:

$$G^0 = \begin{bmatrix} 1/9 & 1/9 & 1/9 \\ 1/9 & 1/9 & 1/9 \\ 1/9 & 1/9 & 1/9 \end{bmatrix}$$

The initial mixed strategies were also initialized to be equal:  $A = \begin{bmatrix} 1/3 \\ 1/3 \\ 1/3 \end{bmatrix}$   $B = \begin{bmatrix} 1/3 & 1/3 & 1/3 \end{bmatrix}$

The following gives the genotype frequencies after 10 generations

$$G^{10} = \begin{bmatrix} 0.1189 & 0.1298 & 0.0909 \\ 0.0995 & 0.1088 & 0.0829 \\ 0.1088 & 0.1416 & 0.1189 \end{bmatrix}.$$

Similarly, the matrices  $G^{50}$  and  $G^{100}$  gives the genotype frequencies after 50, and 100 generations respectively.

$$G^{50} = \begin{bmatrix} 0.1221 & 0.1970 & 0.0283 \\ 0.0463 & 0.0754 & 0.0172 \\ 0.0754 & 0.3163 & 0.1221 \end{bmatrix} \quad G^{100} = \begin{bmatrix} 0.0804 & 0.2113 & 0.0042 \\ 0.0113 & 0.0303 & 0.0015 \\ 0.0303 & 0.5500 & 0.0804 \end{bmatrix}$$

As can be seen from the frequency matrices, the genotype (A3,B2) is clearly overtaking all other combinations in the long run, despite a more gradual change in early generations. As can be seen in the Figures, similar (but less obvious) trends are seen in the mixed strategies at each loci, suggesting prevalence of a (3,2) strategy in the game model as well.

## 5 Conclusions/Discussion

As claimed in *Chastain et al.*, the characteristic similarity of the equations describing the population genetic dynamics and the mixed strategy evolution of the coordination game lead to qualitatively similar results in the simulation. This can be seen in the Figures section, as the mixed strategy profiles look similar to marginal traces of the genotype surfaces for each allele. However, their claims that the multiplicative weight update (i.e. replicator dynamics) "converge to Nash Equilibria if the game is zero sum" are disputed theoretically by *Meir and Parkes*. In their paper, while they concur with regard to the qualitative similarities in behavior, they also emphasize that "the next step of the [MWUA] [...] algorithm and the population dynamics would only be approximately equivalent."

The results of the simulations carried out in this project, are in accord with another observation by Meir and Parkes, which is that: "The approximation becomes less accurate in each step, and in fact even under weak selection the population dynamics may diverge from the Wright manifold, or converge to a different outcome." Meir and Parks also conclude that the assumptions made by Chastain et al. hold only for marginal frequencies, and these are analogous to mixed strategy profiles in the coordination game. Thus, whilst the analogy between population genetic dynamics potentially holds for each allele, it does not necessarily hold for the distribution of all genotypes. It is also worth noting that replicating sample output is difficult given lack of sample code or details as to how the algorithms presented in the paper were actually implemented, including efforts to manage roundoff error, and rationale behind choice of initialization values. This may explain an apparent discrepancy, which is that for certain genotype pairs in this simulation's results, specifically those with the same fitness values, the frequencies are always the same. However, in *Chastain et al.*'s sample output this is not the case despite using the same equation and fitness values/initialization. It is unclear how to resolve this discrepancy without further explanation as to how the sample output was generated.

In context, while these results draw into question the extent and reliability of the two algorithms' implementations, the qualitative similarities still reinforce the analogies between the theoretical frameworks of population genetics and evolutionary game theory. Given that models in the latter area are usually restricted to interactions at higher scales (i.e. between individuals in a population, or individual vs. population, etc.), it is interesting to view a biological phenomenon such as selection at the genetic level by considering genetic loci to be "rational" players optimizing an outcome (i.e., fitness as utility).

## 6 References

Chastain, E., et al. "Algorithms, Games, and Evolution." *Proceedings of the National Academy of Sciences*, vol. 111, no. 29, 2014, pp. 10620–10623., doi:10.1073/pnas.1406556111.

Meir, Reshef, and David Parkes. On Sex, Evolution, and the Multiplicative Weights Update Algorithm. 2015. EBSCOhost, [search.ebscohost.com/login.aspx?direct=true&db=edsarx&AN=edsarx.1502.05056&site=eds-livescope=site](http://search.ebscohost.com/login.aspx?direct=true&db=edsarx&AN=edsarx.1502.05056&site=eds-livescope=site).

## 7 Figures

This section includes summary figures for both the MWUA and Population genetics simulations after 100 generations (timesteps). Note that this is much further than the simulations given in *Chastain et al.* where sample output for only 10 timesteps/generations are given.

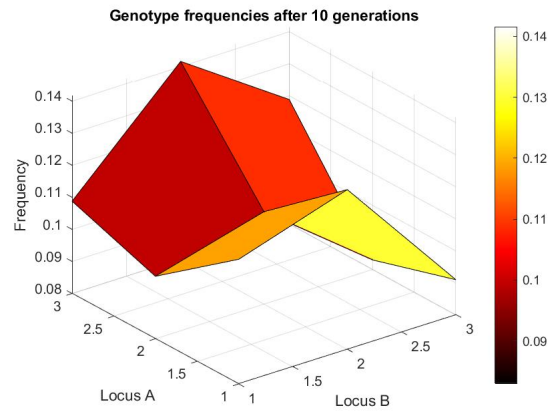


Figure 1: This surface shows the genotype frequencies after 10 generations. Compare to sample output in *Chastain et al.*

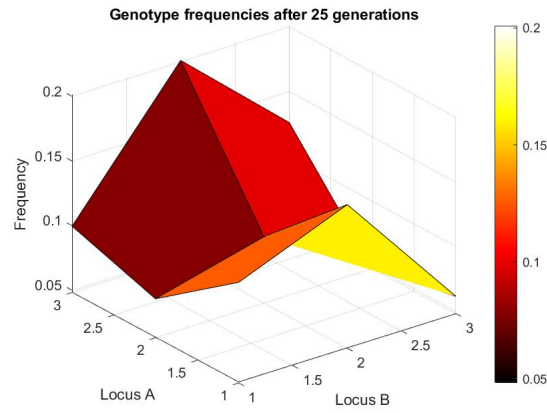


Figure 2: This surface represents the genotype frequencies  $g_{ij}$  after 25 generations

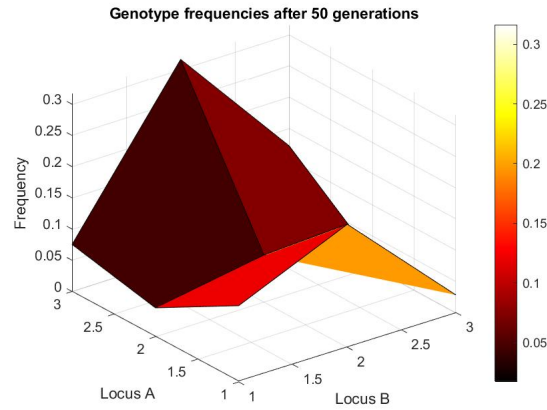


Figure 3: This surface represents the genotype frequencies  $g_{ij}$  after 50 generations.

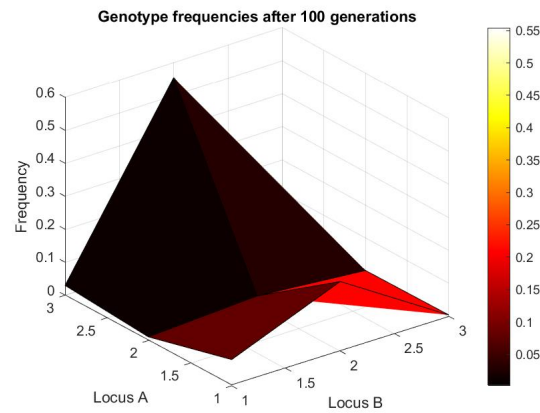


Figure 4: This surface represents the genotype frequencies  $g_{ij}$  after 100 generations. As is visually apparent, the genotype (A3,B2) appears to dominate over time, with all others tending towards 0.

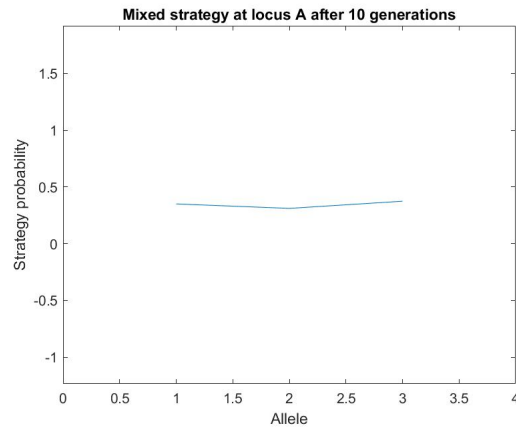


Figure 5: This graph shows the mixed strategy profile at locus A after 10 rounds (generations) These are used for comparison to sample output.

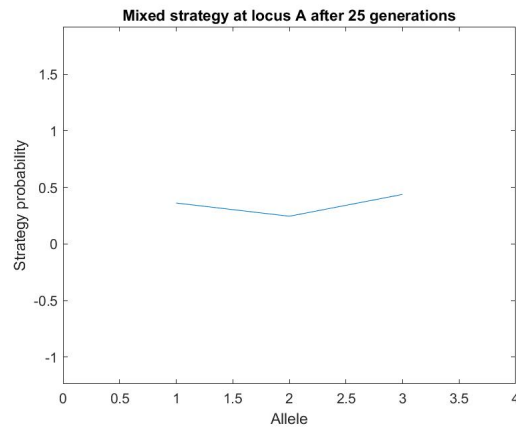


Figure 6: This graph shows the mixed strategy profile at locus A after 25 rounds.

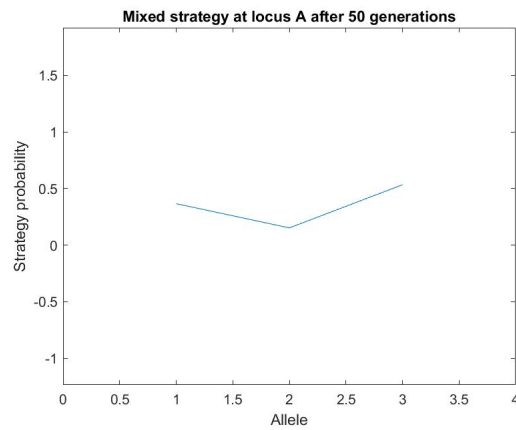


Figure 7: This graph shows the mixed strategy at locus A after 50 rounds (generations)

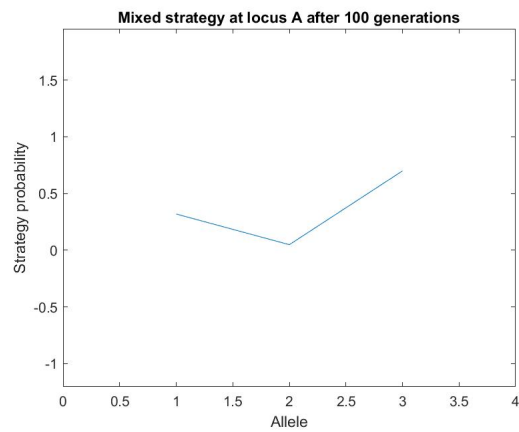


Figure 8: This graph shows the mixed strategy profile for locus A after 100 rounds.

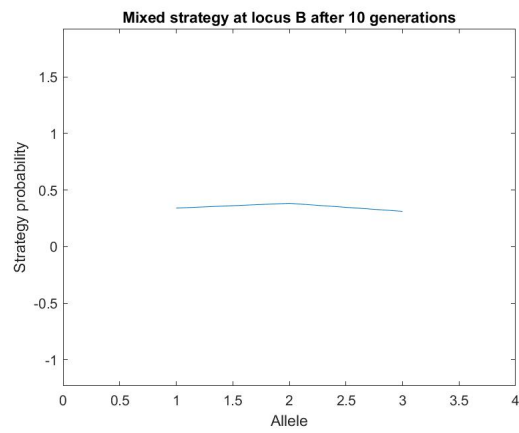


Figure 9: This graph shows the mixed strategy profile for locus B after 10 rounds. Compare to sample output.

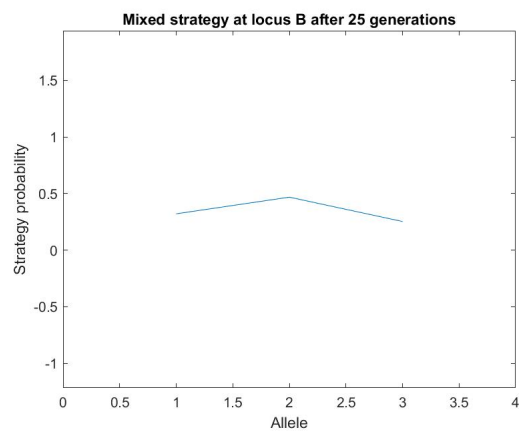


Figure 10: This graph shows the mixed strategy profile at locus B after 25 rounds.



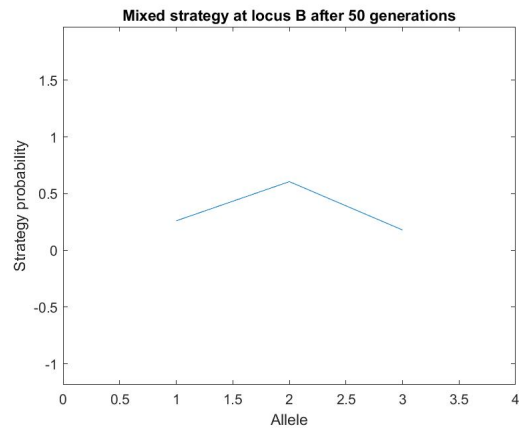


Figure 11: This graph shows the mixed strategy profile for locus B after 50 rounds.

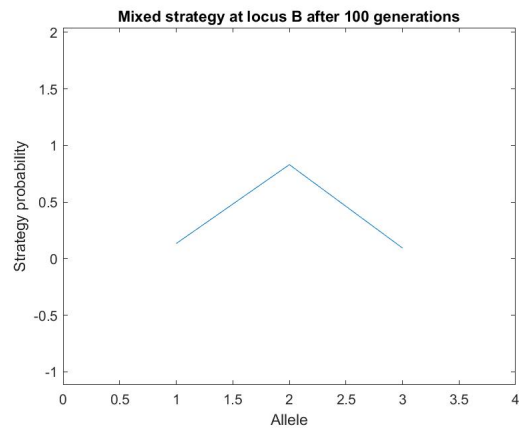


Figure 12: This graph shows the mixed strategy profile for locus B after 100 rounds.