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# Coexistence of Multi-allelic Polymorphism with Migration and Selection

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## Abstract

Population ecology is concerned with the growth patterns of populations. This field has many applications, ranging from survival at the environmental level, to the spread of infectious diseases at the cellular level. Mathematical modeling and computer simulation can be powerful tools in researching this area. I will be investigating the spatial patterns in populations (or gene frequencies) due to migration and selection. My research conditions are for the maintenance of polymorphism under a variety of migration schemes in discrete-space and continuous-time mathematical models. The results will be applicable from the ecological level to the molecular level. Some species are better at adapting to a certain environment and evolve more quickly to fill a niche (*specialists*). Other species are less capable of adapting to their environment (*generalists*). Generalists survive when immigration between two distinct populations of similar species occurs. For example, species A, B, and C all coexist on two distinct islands. Species A is better adapted to shade and species C is better adapted to light; species B is in-between. If island 1 has shade, and island 2 does not, then we would expect only species A to survive on island 1, and only species C on island 2. However, under immigration all species could survive and coexist. This could be a major factor in helping maintain and manage diverse species. We will use our understanding of populations to create mathematical models and computer simulations that will demonstrate this phenomenon and help us to gain an understanding of the principles behind the concepts.

**Keywords: Migration, Selection, Coexistence**

## 1. Introduction

Using computers to model populations has been a growing field ever since Richard Dawkins developed the “Biomorphs” program<sup>4</sup>. This program showed how randomly selected events can lead to a certain endpoint. Computers have come very far since then and can now simulate generations of populations over time with a simple program. Research using computer-based models will help keep bringing together the expanding fields of mathematics, computer science, and biology.

The first published work done with evolution was by Charles Darwin. The study of domesticated plants and animals suggests how and why speciations can occur<sup>1</sup>. Using some of the same concepts introduced, computers can be used to predict certain evolutionary outcomes. Math and computers have worked harmoniously to model everything from viral diseases to forest growth patterns<sup>3</sup>. For example using information about competition can demonstrate how speciation can save a species.

Mathematical models in similar topics have been created for several different scenarios, including two species populations and populations with predation relationships. It is also suggested that allele interactions can function in the same way as species interactions<sup>5</sup>. Using computer software, models were run predicting different biological scenarios.

Every species and allele undergoes selection forces. These forces make species adapt to their surroundings and drive alleles towards homogeneity. Some species or alleles, known as specialists, are better adapted to a certain environment and adapt more quickly to fill an open niche. Other species or alleles, that are less capable of adapting to a certain environment, are known as generalists. These species and alleles can adapt to fit their surroundings as well, but do so more slowly. Over time specialists will always out-compete generalists and drive them towards extinction or speciation. Speciation allows the generalists to specialize in a different niche. These trends are explained by the competitive exclusion principle. This paper will investigate these trends by creating mathematical models.

## 2. Methodology

Models were run using Berkeley-Madonna software. This software uses a mathematical equation and known values to produce a graph that runs over time. Every model that was run increased the understanding of the forces that drive selection in populations of more than one species. Finding a result to summarize the models run helped demonstrate the relationships that happen in the wild.

The Berkeley-Madonna software provided many tools, among these were sliders. Sliders were used to analyze the affects of birth rate and the affects of competition on species survival. The sliders provided easy ways to change the value of a variable without having to create a new model.

Six equations were set up to model three species on two separate patches. Known equations to model species undergoing competition were used<sup>5</sup>. Each species (V, W, X) was given an initial value, a birth rate, a competition rate, and a threshold.

### 3. Data

The primary goal was to set up a computer model for several different situations of animal populations. For every simulation that was run, results were compared to see which method would work better at propagating the generalist species. Understanding the relationships of generalists and specialists, and competition rates and birthrates, could help biologists figure out the best way to work with populations.

Equation 1 was used as a starting point to run models. Equation 4 was used as a general representation for modeling competing species over time. When the equation was set to 0, we found the species could coexist at equilibrium. If the equation was not set to 0 other results could be found, including one species outcompeting the others, or two species coexisting at equilibrium.

$$Dp_{i,k}/dt = \sum \mu_{ki} p_{i,l} + p_{i,k} [\sum r_{i,j,k} p_{j,k} - \sum r_{i,j,k} p_{j,k} p_{j,k}] \quad (1)$$

$$Dp_{i,k}/dt = \sum \mu_{ki} p_{i,l} + p_{i,k} [s_{i,k} - s_k], s_k = \sum r_{i,j,k} p_{j,k} p_{j,k} \quad (2)$$

$$Dp_{i,k}/dt = q \sum \mu_{ki} p_{i,l} + \lambda p_{i,k} [s_{i,k} - s_k] \quad (3)$$

$$Dp_{i,k}/dt = \sum \mu_{ki} p_{i,l} + \lambda p_{i,k} \{ [s_{i,k}(p^{(k)})] - s(p^{(k)}) \} \quad (4)$$

Equation 5 was used to run all two-species models, where S is the number of individuals in the species, b is the birth rate, T is the threshold, c is the competition rate, i is the species being modeled, j is the second competing species, and k is the third competing species<sup>2,6</sup>.

$$\begin{aligned} dp_{i,k}/dt &= \sum \mu_{ki} p_{i,l} + \lambda p_{i,k} \{ [s_{i,k}(p^{(k)})] - s(p^{(k)}) \} \\ \lambda p_{i,k} &= 1/T_i \\ dp_{i,k}/dt &= \sum \mu_{ki} p_{i,l} + \{ [s_{i,k}(p^{(k)})] - s(p^{(k)}) \} / T_i \\ p_{i,k} &= S_i \\ d/dt(S_i) &= \sum \mu_{ki} p_{i,l} + \{ [s_{i,k}(p^{(k)})] - s(p^{(k)}) \} / T_i \\ \sum \mu_{ki} p_{i,l} &= b_i S_i(x) - (x) \\ d/dt(S_i) &= b_i S_i + \{ [s_{i,k}(p^{(k)})] - s(p^{(k)}) \} / T_i \\ x &= p_{i,k} [s_{i,k}(p^{(k)})] - s(p^{(k)}) / T_i \\ d/dt(S_i) &= b_i S_i \{ [s_{i,k}(p^{(k)})] - s(p^{(k)}) \} / T_i \\ p_{i,k} [s_{i,k}(p^{(k)})] - s(p^{(k)}) &= (T_i - S_i - c_i S_j - c_i S_k) \\ d/dt(S_i) &= b_i S_i (T_i - S_i - c_i S_j - c_i S_k) / T_i \\ d/dt(S_i) &= b_i S_i ((T_i - S_i - c_i S_j - c_i S_k) / T_i) \end{aligned} \quad (5)$$

Table 1. Representation of three species on two separate islands undergoing competition without migration. Initial values, birth rate, competition rate and threshold provided.

Island	Species	Initial Value	Birth Rate	Competition Rate	Threshold
1	V	200	0.9	0.2	800

1	W	200	0.7	0.7	550
1	X	200	0.2	0.9	700
2	V	200	0.4	0.8	550
2	W	200	0.7	0.7	550
2	X	200	0.8	0.4	800

Table 2. Equations representing three species undergoing migration over time. Initial values, birth rates, competition rates, and thresholds provided.

Species	Initial Value	Birth Rate	Competition Rate	Threshold
V and U	200	0.65	0.5	1350
W and Y	200	0.7	0.7	1100
X and Z	200	0.5	0.65	1500

#### 4. Conclusions

This research helped predict the time to species extinction. If all values of a particular system were known this model could predict the time to species or allele exclusion. Future experiments could be made to find species competition rates using this research. An environment could be created to model species competition. As a particular species was excluded over time, the total number of individuals should be known over time, and curves can be created. Assuming threshold and birthrate are known values, these curves would show the competition rate. This research also demonstrates how speciation saves a species. As the competition rate approaches 0, each species approaches its particular threshold. This shows that as species compete for less and less resources (speciate) they have an increased survival rate.

Using computers to mathematically model biological systems also helps find conclusions without sacrificing animals. In the “Race to Stockholm” several thousands of animals were slaughtered to find the make-up of one hormone <sup>7</sup>. It is much easier to figure out the make-up of a hormone by running models that describe the way the hormone functions and can predict what the hormone will look like before any lab work is done.

The competition rate had the greatest impact on the eventual outcome. Altering the competition rate created situations in which only one species or allele survived, and also created situations in which all three species or alleles survived. At a competition rate of 0.0 all three species or alleles coexisted. This indicated that if the alleles or species filled different niches than all could coexist. When the average competition rate was higher for the generalist than for the specialist, only two species survived when migration was introduced (Figure 1). When the average competition rate of the generalist was lower than the average competition rate of both specialists, all three species survived (Figure 2).

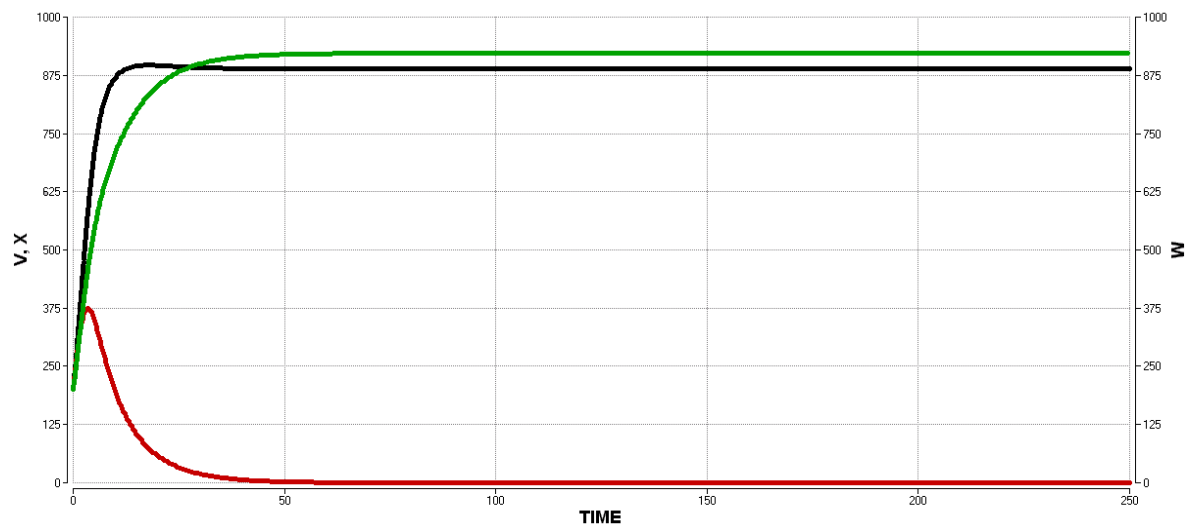


Figure 1. Berkeley-Madonna model run over time with the x-axis showing time and y-axis showing number of individuals. The generalist species does not have lowest average competition rate and was outcompeted by the specialists.

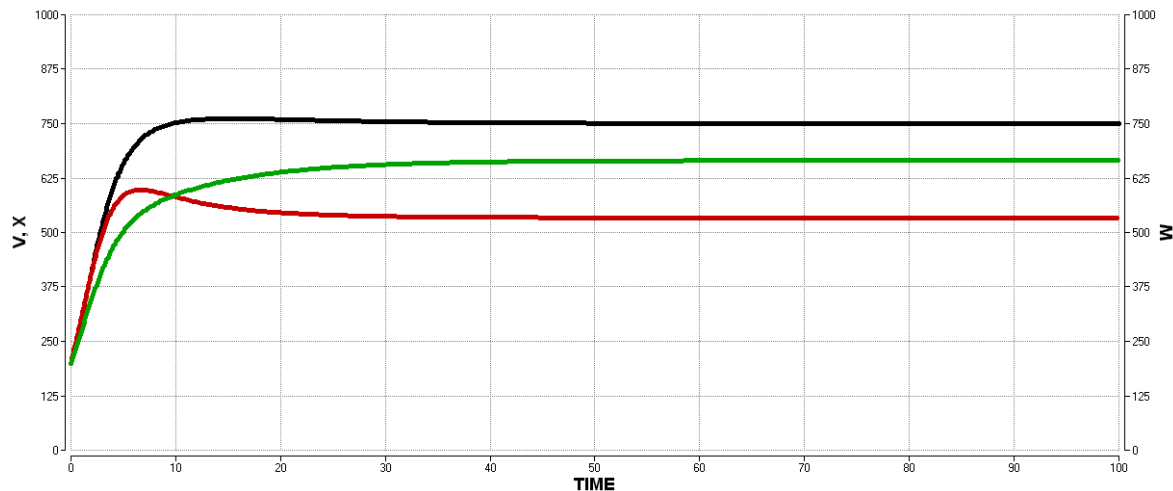


Figure 2. Berkeley-Madonna model run over time with x-axis showing time and y-axis showing number of individuals. The generalist species has lowest average competition rate and survived at equilibrium with the specialists.

It was found that the affects of competition were greater than the affects of birthrate of a species. When the birthrate was increased of a particular species, the curve to the overall outcome changed; however, the endpoints for each species did not change with one exception. As the birthrate of a species approached 0, that species stayed closer to the initial value rather than declining over time. When the birthrate was set at 0 the species maintained the initial population over time. This indicated that there was a problem in either the software or the equation. Future testing should be done to investigate this conclusion.

Being able to calculate the competition rate and birth rate of any particular species will help us determine the rate at which they will die off. This data can be used to find an absolute timeframe for speciation to occur. That is to say, we can predict the amount of time a species has to fill a different niche before it will become extinct.

This research can be applied to multiple scenarios. In the wild it is unusual that only 2 species should compete for the same resources. More species should be accounted for to create more accurate models. It is also unlikely that only two patches should be accounted for.

## 5. Acknowledgements

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