

The lizard project

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1 Exercise 1

1.a) How have the fitness values in the matrix been determined? Why are all the diagonal elements equal to 1.0?

The fitness values in the matrix have been determined with the method described in Lande&Arnold (1983, Evolution). This method, however, appears to assume that the relation between phenotype (throat color) and fitness proxy (number of females monopolized and shared) are additive (for example, the fitness of the orange morph is high when there is a high blue morph density). In this system, that assumption does not hold (for example, the fitness of the orange morph is high when there is a high blue morph density and there is a low yellow morph density).

The diagonals are 1.0, because Sinervo&Lively assume each morph to have a relative fitness of 1.0 to itself. This assumes each morph has the same density-dependent effect on itself.

1.b) Calculate the fitness of the three morphs and the mean fitness of the population for the special case $p_Y = 0.2$, $p_B = 0.3$, $p_O = 0.5$. Which morph has the highest fitness?

Calculating the absolute fitness:

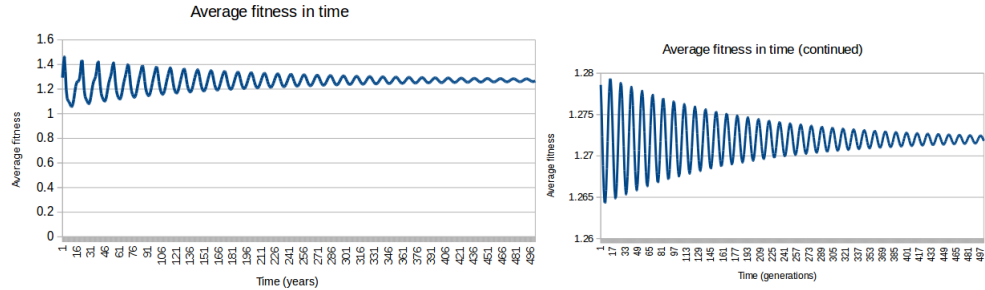
$$\begin{pmatrix} w'_Y \\ w'_B \\ w'_O \end{pmatrix} = \begin{pmatrix} 1 & w_{YB} & w_{YO} \\ w_{BY} & 1 & w_{BO} \\ w_{OY} & w_{OB} & 1 \end{pmatrix} \begin{pmatrix} p_Y \\ p_B \\ p_O \end{pmatrix} = \begin{pmatrix} 1 & 1 & 2 \\ 2 & 1 & 0.1 \\ 0.3 & 4 & 1 \end{pmatrix} \begin{pmatrix} 0.2 \\ 0.3 \\ 0.5 \end{pmatrix} = \begin{pmatrix} 1.5 \\ 0.75 \\ 1.76 \end{pmatrix}$$

The heighest absolute fitness is for the orange morphs, with a value of 1.76.

$$\bar{w} = \sum p_i \cdot w_i = \begin{pmatrix} p_Y \\ p_B \\ p_O \end{pmatrix} \cdot \begin{pmatrix} w'_Y \\ w'_B \\ w'_O \end{pmatrix} = \begin{pmatrix} 0.2 \\ 0.3 \\ 0.5 \end{pmatrix} \cdot \begin{pmatrix} 1.5 \\ 0.75 \\ 1.76 \end{pmatrix} = 1.405$$

1.c) Show that the system converges to an equilibrium at which all three morphs have the same fitness

The system consists out of damped oscillations:

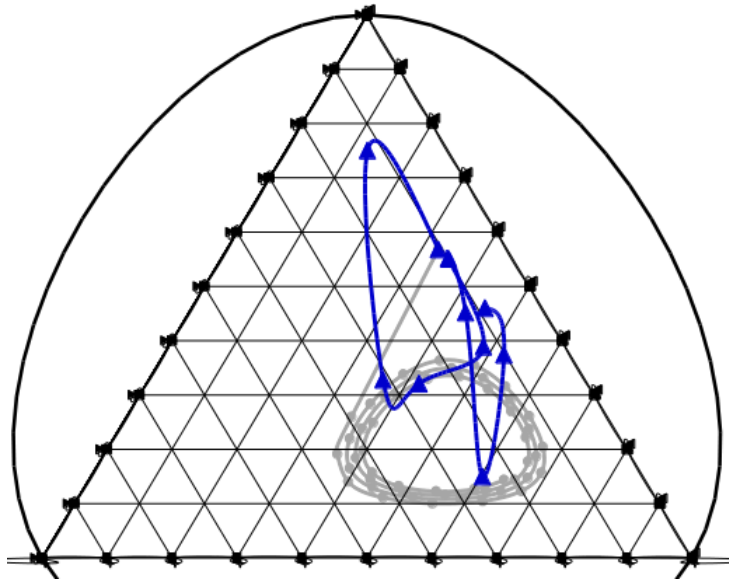


The system converges to (found by numeric approximation in a spreadsheet):

$$\begin{pmatrix} p_Y^* \\ p_B^* \\ p_o^* \end{pmatrix} = \begin{pmatrix} 0.52 \\ 0.21 \\ 0.28 \end{pmatrix}$$

1.d) Check whether the model predictions plotted agree with your own predictions. Do you agree with Sinervo and Lively that the model provides a satisfactory explanation for the pattern found in nature? Why/why not?

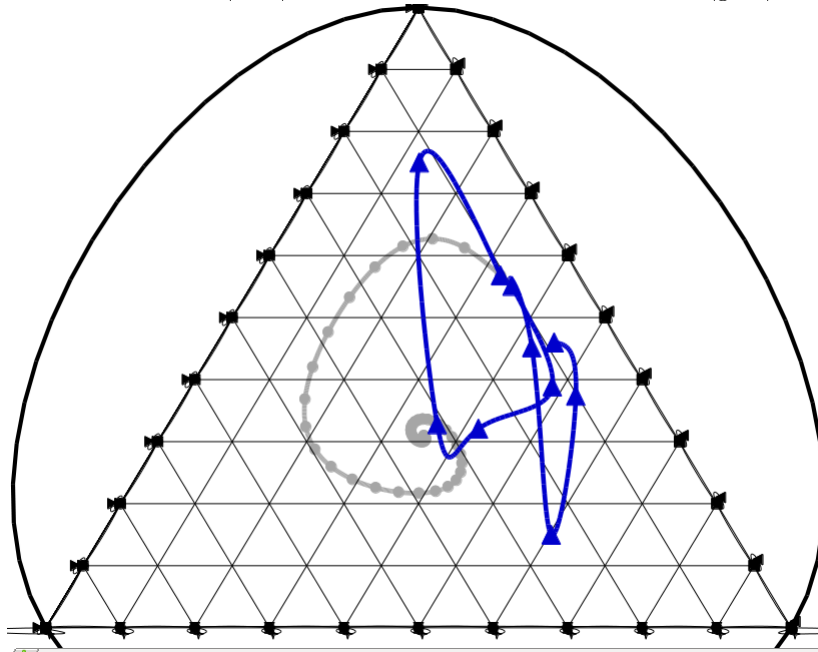
Plotting Sinervo's measured frequencies of 1990 ($\begin{pmatrix} p_Y \\ p_B \\ p_o \end{pmatrix} = \begin{pmatrix} 0.33 \\ 0.57 \\ 0.11 \end{pmatrix}$) the frequencies measured (blue) do not match the values predicted (grey).



Also, when choosing values of later years, the model its predictions never match the observed frequencies of two years later. The system slowly converges to an equilibrium.

1.e) Repeat your simulations, but now for the improved fitness estimates by Sinervo. Do they yield a better fit to the data?

Plotting Sinervo's measured frequencies of 1990 ($\begin{pmatrix} p_Y \\ p_B \\ p_o \end{pmatrix} = \begin{pmatrix} 0.33 \\ 0.57 \\ 0.11 \end{pmatrix}$) the frequencies measured (blue) do not match the values predicted (grey).



Also, when choosing values of later years, the model its predictions never match the observed frequencies of two years later. Additionally, the system converges stronger towards a stable equilibrium, which -in my opinion- lessens the chance the model could potentially fit the data observed.

1.f) What is their main argument for using the replicator dynamics nevertheless? Are you convinced by their argument?

They use the replicator equation, because they assume $h^2 = 1$ ¹, as is the case in asexuals. They do this, as they measured $h^2 = 0.96$ from a regression². This regression actually yielded a $h^2 = 0.48$, yet, 'because they only measured males,

¹bottom-right of page 242

²see figure 3

which only contribute to half of the gametes, they extrapolate it by a factor of two (instead of measuring the females)³.

Yet, this method is commonly done for traits that have a natural order⁴ (for example, tail length). In this example, the scores assigned to the three phenotypes are chosen arbitrarily.

Exercise 2

Payoff matrix of 1996

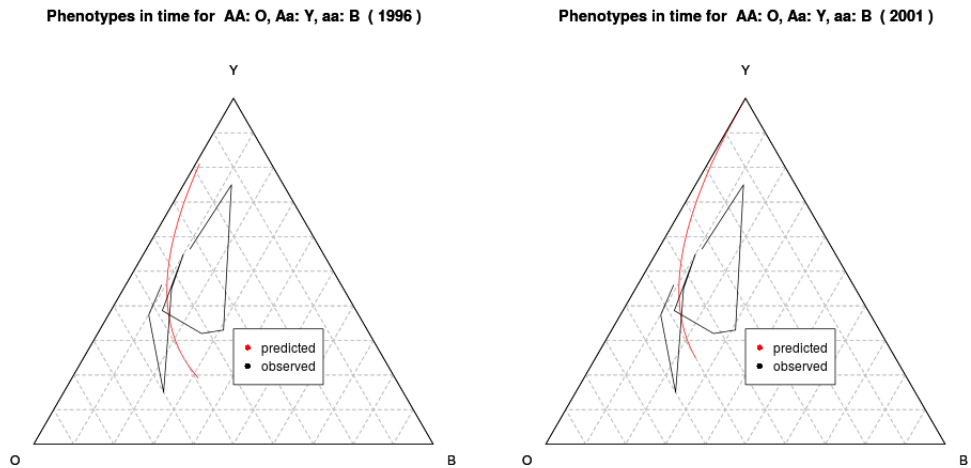
2.a) One locus, two alleles

In all coming scenario's, I expect no oscillations: the equations are similar to the ones we used when discussing the Replicator Equation and Fisher's Fundamental Theorem. In this setup (one locus, two alleles), the population will follow the Hardy-Weinberg line on a triplot. The calculations of these examples were identical to these.

2.a.1) Scenario 1: $AA = O$, $Aa = Y$, $aa = B$

For the data of 1996, the population will fluidly move to a stable coexistence of the three morphs, independent of the initial genotype distribution.

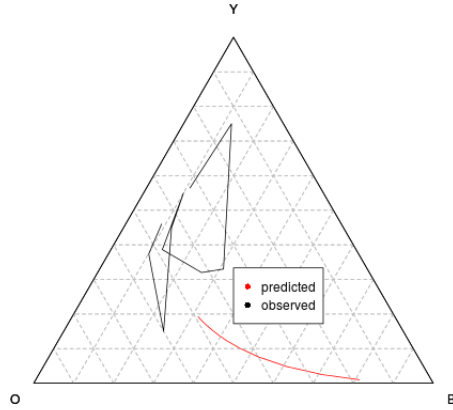
For the data of 2001, the population will fluidly go towards a population with blue morphs only, independent of the initial genotype distribution.



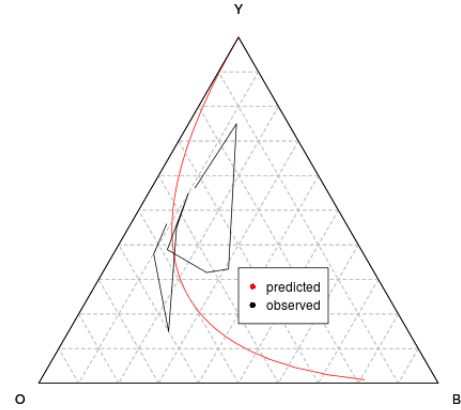
³FJ Weissing, personal communication

⁴FJ Weissing, personal communication

Phenotypes in time for AA: O, Aa: Y, aa: B (1996)



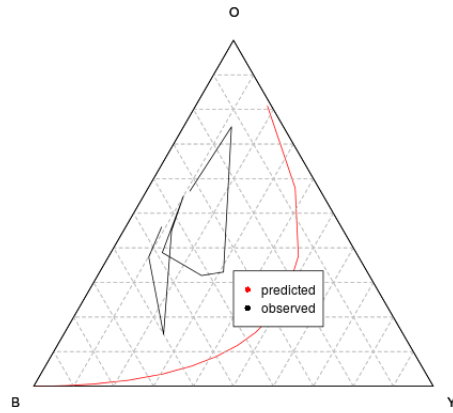
Phenotypes in time for AA: O, Aa: Y, aa: B (2001)



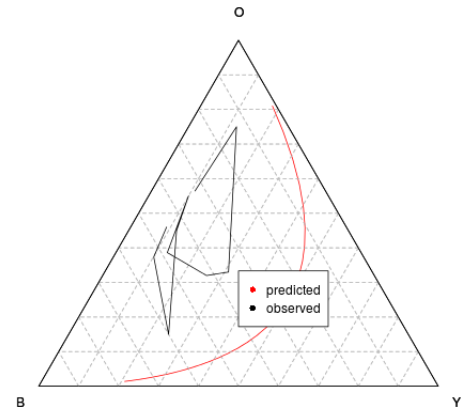
2.a.2) Scenario 2: AA = B, Aa = O, aa = Y

When the heterozygote corresponds to the orange phenotype, the population will become monomorphous for yellow. This is independent of the initial frequency of the A allele. This behavior is the same for both datasets.

Phenotypes in time for AA: B, Aa: O, aa: Y (1996)



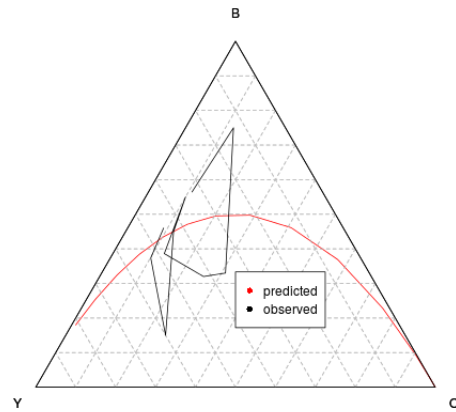
Phenotypes in time for AA: B, Aa: O, aa: Y (2001)



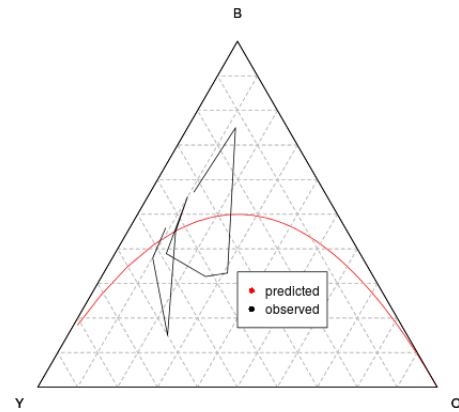
2.a.3) Scenario 3: AA = Y, Aa = B, aa = O

When the heterozygote corresponds to the blue phenotype, the population will become monomorphous for orange. This is independent of the initial frequency of the A allele. This behavior is the same for both datasets.

Phenotypes in time for AA: Y, Aa: B, aa: O (1996)



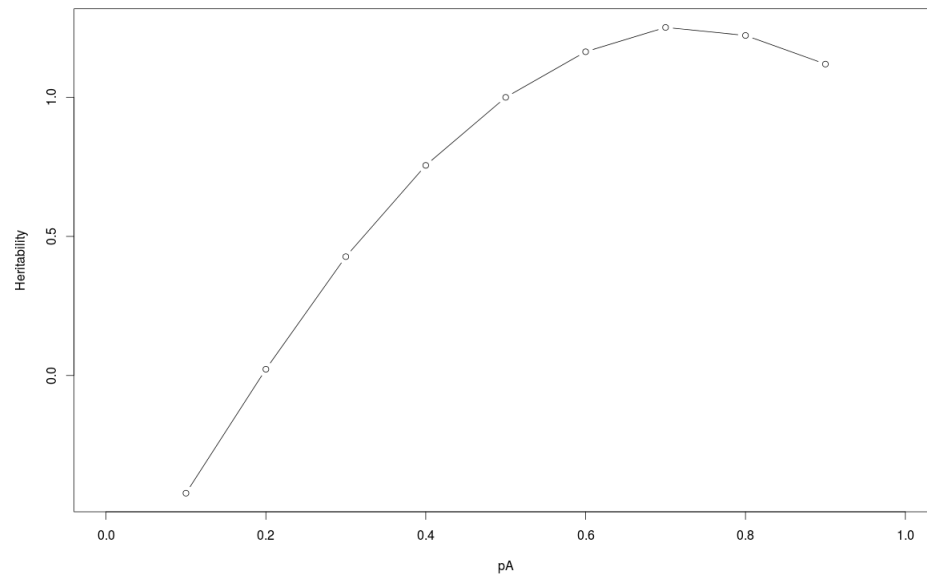
Phenotypes in time for AA: Y, Aa: B, aa: O (2001)



2.a.4) Heritabilities

Heritability is dependent on the environment. There is no such thing as a heritability of x that is the same in all environments. I tried to calculate the heritabilities according to FJW's explanation. Except for the data point pre-calculated, all other data points are off.

Heritabilities for different allele frequencies



2.b) One locus, three alleles

Did not do this.

2.c) One locus, three alleles, partial dominance

Did not do this.

2.d) Considerations

Only in one setup (2.a.1) the payoff matrix of 1996 yielded a prediction that was qualitatively true, namely a stable coexistence of the three morphs. Quantitatively, both payoff matrices are very bad predictors.

I cannot tell which genetic system is best, as I've only implemented one. There are still plenty of systems I'd like to investigate, like using multiple loci or infinitely many (quantitative genetics) or epigenetic inheritance of phenotype. I hope that the genetic system of the side-blotched lizard is once elucidated, as it will render many assumptions made obsolete. If I have to choose between models, I'd choose the one locus, three alleles model with partial dominance, as I expect that genetics plays a minor role, and this model has the most potential for adding randomness into it.

Exercise 3

3.a) Payoff matrix

I first created a simpler version based on the payoff matrix in table 1. When using the payoff matrix, you use the following equations:

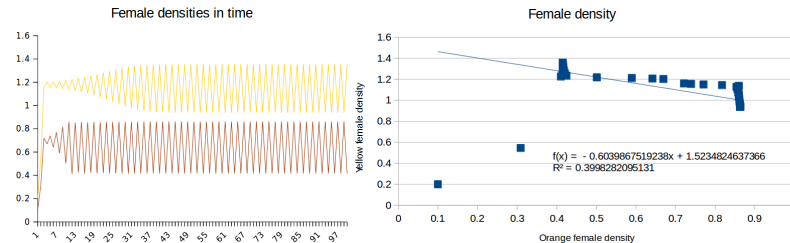
$$N_i(t+1) = N_i(t) + F_i \cdot \frac{w_i(t)}{\bar{w}} \cdot N_i(t) \left(1 - \frac{N_i}{K_i}\right)$$

$$\begin{pmatrix} p_o(t) \\ p_y(t) \end{pmatrix} = \begin{pmatrix} \frac{N_o(t)}{N_o(t)+N_y(t)} \\ \frac{N_y(t)}{N_o(t)+N_y(t)} \end{pmatrix}, \begin{pmatrix} w_o(t) \\ w_y(t) \end{pmatrix} = \begin{pmatrix} 1 & 1.61 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} p_o(t) \\ p_y(t) \end{pmatrix}$$

,

Using the parameters, you get a two-cycle as shown below:

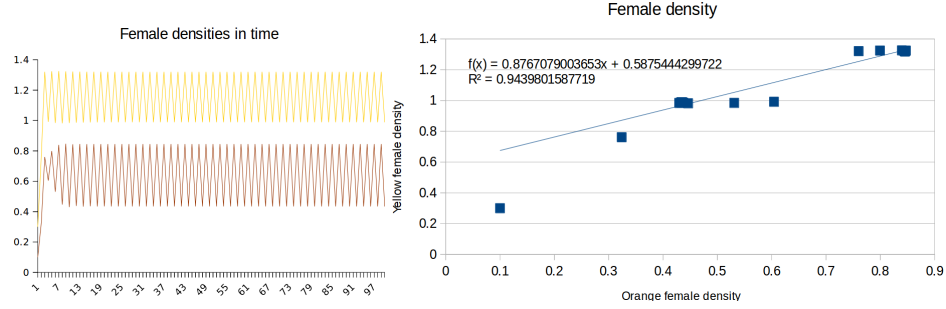
$$N(t=0) = \begin{pmatrix} N_o \\ N_y \end{pmatrix} = \begin{pmatrix} 0.1 \\ 0.2 \end{pmatrix}, \begin{pmatrix} F_o \\ F_y \end{pmatrix} = \begin{pmatrix} 2.2 \\ 2.2 \end{pmatrix}, \begin{pmatrix} K_o \\ K_y \end{pmatrix} = \begin{pmatrix} 0.7 \\ 1.18 \end{pmatrix}$$



In the figures above, a high density of one species occurs simultaneously with a low density of the other.

When using the initial densities below, this evasion game changes to a coordination game, in which both morphs are both either at high or both at low densities:

$$N(t = 0) = \begin{pmatrix} N_o \\ N_y \end{pmatrix} = \begin{pmatrix} 0.1 \\ 0.3 \end{pmatrix}$$



3.b+c) Discrete logistic ESS model

When using the fitness formula's below table 1, you use the following equations:

$$N_i(t + 1) = N_i(t) + F_i \cdot \frac{w_i(t)}{\bar{w}} \cdot N_i(t) \left(1 - \frac{N_i}{K_i} \right)$$

$$N(t) = \sum N_i(t)$$

$$\begin{pmatrix} p_o(t) \\ p_y(t) \end{pmatrix} = \begin{pmatrix} \frac{N_o(t)}{N(t)} \\ \frac{N_y(t)}{N(t)} \end{pmatrix}$$

$$w_{o1} = 0.98 - 0.84N_{oo} + 0.27N_{oy}$$

$$w_{y1} = 1.04 + 0.02N_{yo} - 0.35N_{yy}$$

$$w_{o1,2-5} = 0.18 - 0.38N_{oo} - 0.14N_{oy}$$

$$w_{o12-5} = 0.22 - 0.03N_{yo} - 0.35N_{yy}$$

How N_{oo}, N_{oy}, N_{yo} and N_{yy} are calculated is unknown. What Sinervo does with each of these four equations above is unknown, so I formulate it as such, and will expand this mystery function below:

$$\begin{pmatrix} w_o(t) \\ w_y(t) \end{pmatrix} = \begin{pmatrix} f(w_{o1}(t), w_{o2-5}(t)) \\ f(w_{y1}(t), w_{y2-5}(t)) \end{pmatrix}$$

My hypothesis: N_{ij} = number of born juveniles from gametes with i and j alleles

$$\begin{pmatrix} N_{oo}(t) & 2.N_{oy}(t) \\ 2.N_{oy}(t) & N_{yy}(t) \end{pmatrix} = \begin{pmatrix} p_o(t)p_o(t)N(t) & 2.p_o(t)p_y(t)N(t) \\ 2.p_o(t)p_y(t)N(t) & p_y(t)p_y(t)N(t) \end{pmatrix}$$

My hypothesis: $w_{o1}(t)$ is the fitness of the first egg, $w_{o2-5}(t)$ of all later eggs. Defining E = number of eggs:

$$\begin{pmatrix} E_o \\ E_y \end{pmatrix} = 2 \begin{pmatrix} F_o \\ F_y \end{pmatrix}$$

$$\begin{pmatrix} w_o(t) \\ w_y(t) \end{pmatrix} = \begin{pmatrix} f(w_{o1}(t), w_{o2-5}(t)) \\ f(w_{y1}(t), w_{y2-5}(t)) \end{pmatrix} = \begin{pmatrix} w_{o1}(t) + (E_o - 1)w_{o2-5}(t) \\ w_{y1}(t) + (E_y - 1)w_{y2-5}(t) \end{pmatrix}$$

3.d) Questions oabout discrete logistic ESS model

Can you reconstruct the dynamics observed in figure 4 (top)?

Never.

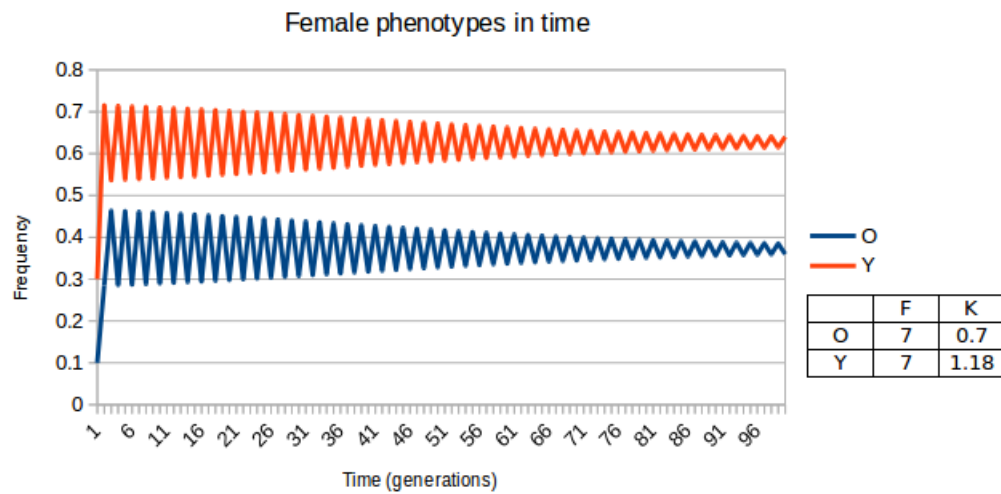
For which values of the parameter F_i do you find stable oscillations of both morphs? Which other outcomes do you observe?

There are three different scenario's that I observed. Using these parameters below:

$$N(t=0) = \begin{pmatrix} N_o \\ N_y \end{pmatrix} = \begin{pmatrix} 0.1 \\ 0.2 \end{pmatrix}, \begin{pmatrix} K_o \\ K_y \end{pmatrix} = \begin{pmatrix} 0.7 \\ 1.18 \end{pmatrix}$$

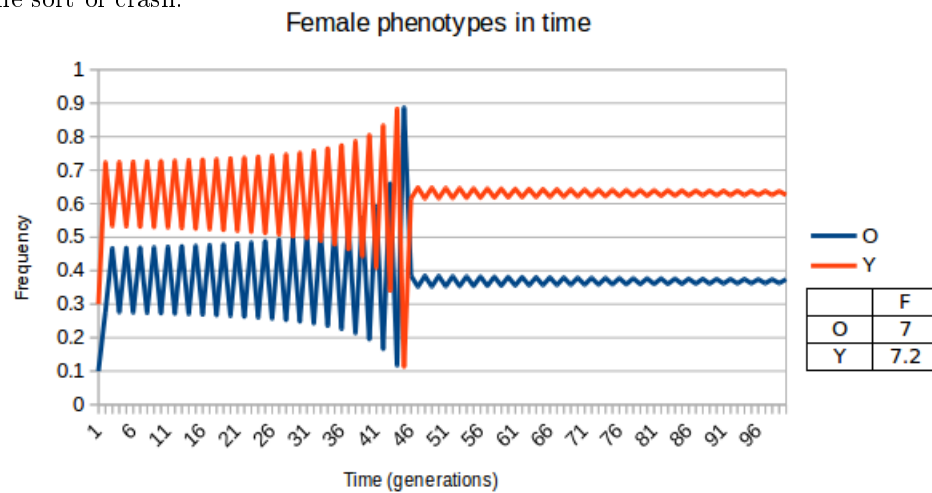
And using different values of $\begin{pmatrix} F_o \\ F_y \end{pmatrix}$ combinations, you get the following scenario's:

Damped oscillations



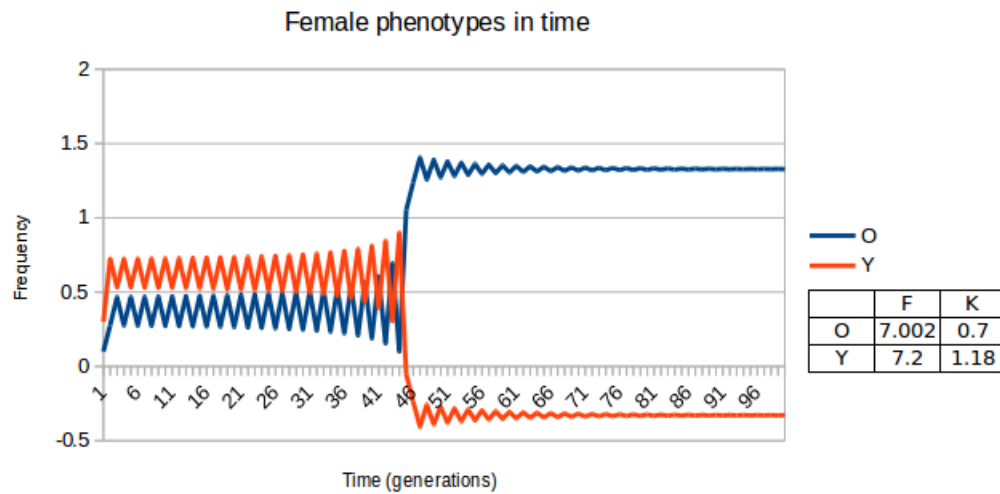
Stable two cycles

There is a narrow range in which the population reaches a stable two-cycle after some sort of crash:



Extinction

Although the model works with frequencies (assuming infinite populations), the population will still lose one morph. Note that F_o is only slightly increased compared to the previous run.



2 Reflection

About 80% of the time was spent on finding out details of the R programming language for exercise 2, instead of doing actual work. Luckily, I did switch to LibreOffice Calc for exercise 3 again. Next time, I will not use R if there is a deadline.

An example of R behaviour that surprised me:

```
# Put a and b in a container
t <- c(a,b)
# Check that the first element in the container is the first element put in
# If these differ , ironically thank the R Development Core Team
if(t[1] != a) { print("Thanks R!") }
```

3 Acknowledgements

Part of this work has improved from collaborations with Francesca Sozzi.