An Extension of the Hassell-Comins Discrete Time Model for Two Competing Species

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Abstract

Multiple discrete time competing species models are looked at including the Leslie-Gowers, Hassell-Comins, and our model. After the Leslie-Gowers and Hassell-Comins models are explored, an extension of the Hassell-Comins model is defined. The equilibria are defined and their conditions for stability are explained. Proofs are given for the instability of $(0, 0)$ and a few conjectures reguarding the stability of equilibria are given that make this model interesting. The differences and importance between this model and the Hassell-Comins model show the importance of the continuation of this research.

1 Introduction

Species not only rely on the resources around them but are also affected by the species in their environment. Species that are in predator-prey situations are not the only ones that are affected by each other. If multiple species are competing for the same resources for survival, the species are affected by the size of the other populations. One species that is more dominant in a environment can cause another species to die off. Modeling these interactions can be useful in controlling an environment. One way of modeling an environment like this is through discrete time competition models. An older model is discussed in order to see the usefulness of a new model that gives light to important aspects in an environment. Many aspects of this model are explained in order to fully understand how this model works including its equilibria, their stability, and conjectures and proofs relating to the model. First the Hassell-Comins Model will be explained including it's equilibria and their stability. Then the new model's equilibria and their stability will be compared. Three conjectures regarding the stability of the equilibria are presented. The paper will then be concluded with areas of future research.

2 The Hassell-Comins Model

Before introducing our new model, the Hassell-Comins model must be understood because the new model is a variation of this model. The Hassell-Comins model, published in 1976 [2], is a variation of the Leslie-Gower logistic model [3]. The Leslie-Gower model played a big part in competition modeling history since it was able to model 2 flour beetle species accurately. It uses discrete time rather than differential equations which can be used for continuous time. Using discrete time instead of continuous time works for population growth since population growth usually change seasonally. For example, reproduction will take place in the warmer months while species will die off more in the colder months. Therefore, yearly, the populations will follow the same trends. The Hassell-Comins model looks very similar to the Leslie-Gowers model but had new parameters b and b'. The Hassell-Comins models consider populations x and y and denote the change over time by considering x_t and y_t against x_{t+1} and y_{t+1}. The model is of the form

$$\begin{cases} x_{t+1} = \frac{x_t}{(r_1+a_{11}x_t+a_{12}y_t)^b} \\ y_{t+1} = \frac{y_t}{(r_2+a_{21}x_t+a_{22}y_t)^{b'}}. \end{cases}$$

Figure 1 shows what a phase diagram of the Hassell-Comins model looks like. The populations are on the axes and there are four different initial conditions represented by the different colors. Where the colors bunch up is where the populations get to the

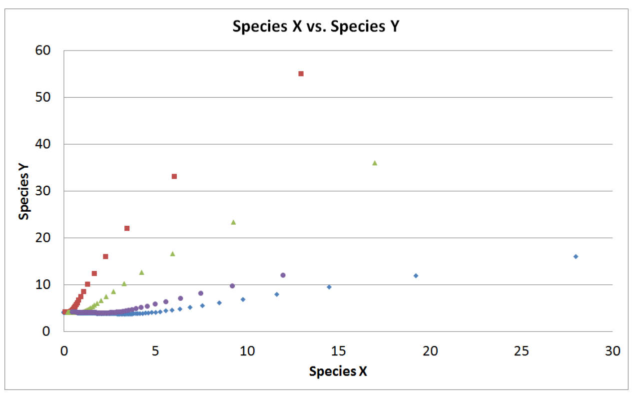

Figure 1: Example of Flow Diagram

equilibrium. In this case, all initial conditions lead to a point on the y-axis. Similar diagrams will be used for our new model, except we chose to use flow curves at which the discrete time model is displayed as a curve.

There are different types of parameters in this model: the a's, r's, and b's. The r's represent the restriction on reproduction ($(1-r_1)$ would facilitate the reproduction rate for the x population). The a's represent the innerspecific and intraspecific competition. The higher the a value, the greater the species will be affected by the according species. The b values represent the speed at which the changes in population take place. The

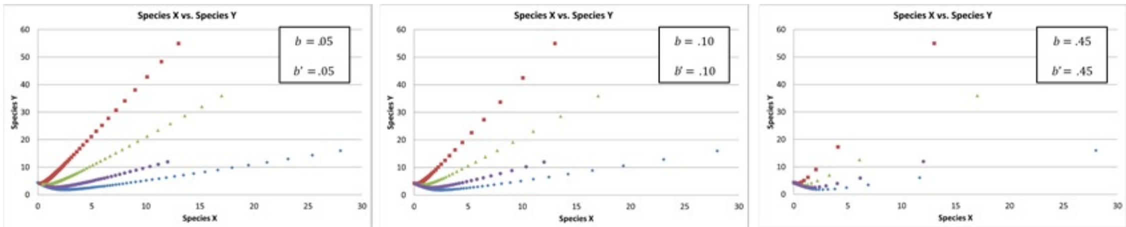

Figure 2: The Impact of Changing b and b'

larger the value, the faster the changes will take place. Figure 1 shows how just a change in the b's can affect the populations. The populations are on the axes showing that the populations approach equilibrium faster as b and b' increase. This can be said since the points are farther apart. The point that the y population reaches is the same in each case. This can be shown by solving for the location of the equilibrium points.

Equilibrium points are the values of (x_t, y_t) in which every $(x_{t+k}, y_{t+k}) = (x_t, y_t)$, when $k > 0$. Therefore, if the populations reach the equilibrium points, the populations will not increase or decrease. The first equilibrium point of this system is at $(x, y) = (0, 0)$ because neither species can change population when they are both 0, since they cannot reproduce. The next two equilibrium points lie on the x-axis and the y-axis. These values are when one of the populations dies off and the other species reaches a steady state. These two points will be referred to as $(x^*, 0)$ and $(0, y^*)$. x^* is found by letting $x_{t+1} = x_t$ and $y = 0$, which gives (1).

$$x^* = \frac{1 - r_1}{a_{11}} \tag{1}$$

y^* is found by letting $y_{t+1} = y_t$ and $x = 0$, and gives (2).

$$y^* = \frac{1 - r_2}{a_{22}} \tag{2}$$

The last equilibrium point $(\bar{x}, \bar{y})$ is when both populations reach a steady state. So both, $x_{t+1} = x_t$ and $y_{t+1} = y_t$.So, simultaneously solving

$$\bar{x} = \frac{1}{(r_1+a_{11}\bar{x}+a_{12}\bar{y})^b}\bar{x}$$
and
$$\bar{y} = \frac{1}{(r_2+a_{21}\bar{x}+a_{22}\bar{y})^{b'}}\bar{y},$$

gives

$$(\bar{x}, \bar{y}) = (\frac{r_2a_{12} - a_{22}r_1 - a_{12} + a_{22}}{a_{11}a_{22} - a_{12}a_{22}}, \frac{r_2a_{11} - a_{21}r_1 - a_{11} + a_{21}}{a_{11}a_{22} - a_{12}a_{22}}). \quad (3)$$

Therefore, all four equilibrium points of a system can be found with the system's coefficients and these above formulas. Though all four equilibria exist in this model no matter the parameter values, they will not all be stable.

An unstable equilibrium point is when a population will not approach the equilibrium unless the population is along an axis or starting at the equilibrium. A stable equilibrium can be reached by either having initial conditions at that point or in some basin of attraction. There will be the same number of basins of attraction as number of stable equilibria since the population will always flow to one of the stable equilibria based on initial conditions. One way of discovering if the equilibrium is stable is looking at the eigenvalues of the Jacobian matrix [4]. The Jacobian is defined as $J(x,y) = \begin{bmatrix} \frac{\partial x_t}{\partial x} & \frac{\partial x_t}{\partial y} \\ \frac{\partial y_t}{\partial x} & \frac{\partial y_t}{\partial y} \end{bmatrix}$. Since $y = 0$ at $(x^*, 0)$, its Jacobian is triangular and its eigenvalues are located on the diagonal. In order for the equilibrium to be stable the eigenvalues must be between -1 and 1. For $(x^*, 0)$ to be stable,

$$\begin{cases} 0 < \frac{1}{a_{21}x+r_2} < 1 \\ 0 < \frac{1}{[r_1+a_{11}x]^b} - \frac{xa_{11}a_{12}}{a_{11}x+a_{21}y+r_1} < 1. \end{cases}$$

Similarly for $(0, y^*)$ to be stable,

$$\begin{cases} 0 < \frac{1}{[r_1+a_{12}y]^b} < 1 \\ 0 < \frac{1}{[r_2+a_{21}y]^{b'}} - \frac{yb'a_{22}}{a_{22}y+r_2} < 1. \end{cases}$$

A more in-depth explanation can be seen in [4]. The Jacobian cannot be used for the point $(0,0)$ but it can be shown that this point is always unstable because when the populations get close enough to the origin, the populations will grow and never reach the origin. The proof of this fact in the new model will be given in Section 5 which also can be applied to the Hassell-Comins model.

For $(\bar{x},\bar{y})$, the Jacobian can be used but finding its Eigenvalues can be more complicated since it is not a triangular matrix. Therefore, looking at a set of isoclines is an easier way of discovering its stability. Isoclines (Figure 2) are the lines at which $x_t = x_{t+1}$ and $y_t = y_{t+1}$. $(\bar{x},\bar{y})$ is stable if these two lines intersect because that is where both $x_t = x_{t+1}$ and $y_t = y_{t+1}$, the conditions for $(\bar{x},\bar{y})$. Figure 2 shows what these isoclines look like when they intersect. From this figure, one can see the necessary

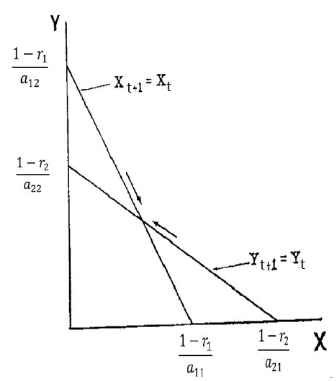

Figure 3: Isoclines

conditions for this to take place. For these lines to intersect, the intercepts must be in a particular order. For example in Figure 2's case, $\frac{1-r_1}{a_{11}} < \frac{1-r_2}{a_{21}}$ and $\frac{1-r_2}{a_{22}} < \frac{1-r_1}{a_{12}}$ forcing the lines to cross. Now with all equilibria's stability necessary conditions defined, we are able to understand the new model. For a more complete explanation of the Hassell-Comins model, refer to [4]. Now that a brief understanding of this model has been done, the new model can now be presented.

3 New model

The new model explored has the equations

$$\begin{cases} x_{t+1} = \frac{x_t}{r_1+a_{11}{x_t}^{b_{11}}+a_{12}{y_t}^{b_{12}}} \\ y_{t+1} = \frac{y_t}{r_2+a_{21}{x_t}^{b_{21}}+a_{22}{y_t}^{b_{22}}}. \end{cases}$$

x_t and y_t represent the populations' sizes at time t. Though this model looks very similar to the Hassell-Comins Model, this model has a variation on the location of the b parameters. In the Hassell-Comins model, there were two b parameters, one on each equation and each controlled the x and the y populations' growth at the same time. In this new model, there are four b parameters. They are the exponents of each of the x and y values. This change was made because the sensitivity of a population towards itself may be different than the sensitivity of another population on that population. For example, a species may react more when three more organisms of a different species are added to a population than if three more organisms of the same species are added. Though this change in the model may be small, since it is dealing with the exponents, it changes the model quite a bit when solving for different aspects of it, including equilibria and their stability. The conditions on the parameters do remain the same as the Hassell-Comins model with $0 < r_i < 1$, $0 < a_{ij} < 1$, and $b_{ij} > 0$. Similar to the Hassell-Comins model, the equilibria are an important part of understanding the model and some will look very similar to the older model.

4 The Equilibrium Points

Like the Hassell-Comins model, the equilibria are denoted by $(0,0)$, $(x^*,0)$, $(0,y^*)$, and $(\bar{x},\bar{y})$.In this model, there is the possibility of having multiple $(\bar{x},\bar{y})$. They will be denoted by $(\bar{x_i},\bar{y_i})$ if more than one exists. Again, $(0,0)$ is when both populations go extinct, $(x^*,0)$ is when the x population becomes dominant, $(0,y^*)$ is when the y population becomes dominant, and $(\bar{x},\bar{y})$ is when both populations can coexist. In order to solve for x^*, x_{t+1} is set equal to x_t and $y_t = 0$ in (4) to get (5). In order to solve for y^*, y_{t+1} is set equal to y_t and $x_t = 0$ in (6) to get (7).

$$x_t = \frac{x_t}{r_1 + a_{11}x^{*b_{11}} + a_{12}0^{b_{12}}} \tag{4}$$

$$x^* = (\frac{1-r_1}{a_{11}})^{b_{11}} \tag{5}$$

$$y_t = \frac{y_t}{r_2 + a_{21}0^{b_{21}} + a_{22}y^{*b_{22}}} \tag{6}$$

$$y^* = (\frac{1-r_2}{a_{22}})^{b_{22}} \tag{7}$$

The final equilibrium point, $(\bar{x},\bar{y})$ is when both populations can live in coexistence. Though this point could be solved for with software in the Hassell-Comins Model, because of the exponents in this model, the point can not be expressed easily. This point is found by setting $x_{t+1} = x_t$ and $y_{t+1} = y_t$. Therefore, $(\bar{x},\bar{y})$ is determined by the simultaneous solution (if any) of

$$1 = r_1 + a_{11}\bar{x}^{b_{11}} + a_{12}{y_t}^{b_{12}}$$

$$1 = r_2 + a_{21}\bar{x}^{b_{21}} + a_{22}{y_t}^{b_{22}}.$$

Though the exact location cannot be expressed, some information about this equilibrium can be understood. Unlike the Hassell-Comins model which has at mos one value for $(\bar{x}, \bar{y})$, because of the exponents in the new model, there can be up to two values for $(\bar{x_i}, \bar{y_i})$. The existence of the equilibria does not guarantee the stability though.

5 The Stability of the Equilibria

Though x^* and y^* exist in every system, the stability of these equilibria is not guaranteed. A stable equilibrium means a population starting nearby will approach the equilibrium and reach the point. An unstable equilibrium means the population will only reach the equilibrium if the population starts at that point or the pertaining axis. It turns out that while $(x^*, 0)$, $(0, y^*)$, and $(\bar{x_i}, \bar{y_i})$ can be either stable or unstable, $(0, 0)$ will always be unstable. That means both populations will never go extinct unless they both start extinct.

Theorem 1: $(0, 0)$ is an unstable equilibria.

In order to show that $(0, 0)$ is always an unstable equilibrium, we must show that when x_t and y_t are small, $x_{t+1} > x_t$ and $y_{t+1} > y_t$. Therefore, we must show that $r_1 + a_{11}x_t^{b_{11}} + a_{12}y_t^{b_{12}} < 1$ and $r_1 + a_{21}x_t^{b_{21}} + a_{22}y_t^{b_{22}} < 1$ for any $0 < r_1 < 1$, $0 < a_{ij} < 1$, $0 < b_{ij}$, and sufficiently small x_t and y_t.

Proof: Fix $0 < r_{ij} < 1$, $0 < a_{ij} < 1$, and $0 < b_{ij}$. Choose possible values of $x_t < (\frac{1-r_1}{2a_{11}})^{\frac{1}{b_{11}}}$ and $y_t < (\frac{1-r_2}{2a_{12}})^{\frac{1}{b_{12}}}$.

$$\begin{aligned}
r_1 + a_{11}x_t^{b_{11}} + a_{12}y_t^{b_{12}} &< r_1 + a_{11}((\frac{1-r_1}{2a_{11}})^{\frac{1}{b_{11}}})^{b_{11}} + a_{12}((\frac{1-r_2}{2a_{22}})^{\frac{1}{b_{12}}})^{b_{12}} \\
&= r_1 + a_{11}(\frac{1-r_1}{2a_{11}}) + a_{12}(\frac{1-r_2}{2a_{22}}) \\
&= r_1 + (\frac{1-r_1}{2}) + (\frac{1-r_2}{2}) \\
&= r_1 - \frac{r_1}{2} + \frac{1}{2} + \frac{1}{2} - \frac{r_2}{2} \\
&= 1 + \frac{1}{2}(r_1 - r_2) < 1.
\end{aligned}$$

Now, choose $x_t < (\frac{1-r_1}{2a_{21}})^{\frac{1}{b_{21}}}$ and $y_t < (\frac{1-r_2}{2a_{22}})^{\frac{1}{b_{22}}}$. Then,

$$\begin{aligned}
r_2 + a_{21}x_t^{b_{21}} + a_{22}y_t^{b_{22}} &< r_2 + a_{21}((\frac{1-r_1}{2a_{21}})^{\frac{1}{b_{21}}})^{b_{21}} + a_{22}((\frac{1-r_2}{2a_{22}})^{\frac{1}{b_{22}}})^{b_{22}} \\
&= r_2 + a_{21}(\frac{1-r_1}{2a_{21}}) + a_{22}(\frac{1-r_2}{2a_{22}}) \\
&= r_2 + (\frac{1-r_1}{2}) + (\frac{1-r_2}{2}) \\
&= r_2 - \frac{r_1}{2} + \frac{1}{2} + \frac{1}{2} - \frac{r_2}{2} \\
&= 1 + \frac{1}{2}(r_2 - r_1) < 1. \blacksquare
\end{aligned}$$

Thus, it is shown that $(0,0)$ will always be an unstable equilibrium in this model.

The stability of $(x^*,0)$ and $(0,y^*)$ can be determined by looking at the eigenvalues of the Jacobian.

The matrix for both x^* and y^* are triangular matrices since the other variable is set to 0 in both situations. Therefore, for $(x^*,0)$ to be stable, both of the following conditions must be true

$$\begin{cases} (\frac{1-r_1}{a_{11}})^{\frac{1}{b_{11}}} > (\frac{1-r_2}{a_{21}})^{\frac{1}{b_{21}}} \\ 0 < b_{11}(1-r_1) < 2. \end{cases}$$

In order for $(0,y^*)$ to be stable, both of the following conditions must be true

$$\begin{cases} (\frac{1-r_2}{a_{22}})^{\frac{1}{b_{22}}} > (\frac{1-r_1}{a_{12}})^{\frac{1}{b_{12}}} \\ 0 < b_{22}(1-r_2) < 2. \end{cases}$$

The first condition for each point can be explained biologically by the component of the reproduction rate $1-r_i$ needs to be large and the sensitivity a_{ii} towards itself needs to be small for a population for that population to dominate over another. The second condition shows that the sensitivity rate of the population towards itself and the reproduction rate component cannot be too large in order for the population to dominate. As long as $b_{11} < 2$ and $b_{22} < 2$, this condition will always be met since $0 < r_i < 1$. Therefore, one way this model works well is that the stability of the equilibria can be explained biologically.

The stability of $(\bar{x}, \bar{y})$ cannot be readily found using a Jacobian, even if the point's location could be simplified, because neither population is set to 0 so the Jacobian will not be triangular. Again, programming could be used to find the eigenvalues but just like the point itself, the expressions are too complicated to make sense of. In order to understand the stability of this system more, simulations can help one see trends in the model.

Theorem 2: When $(\bar{x}, \bar{y})$ exists, $\bar{x_i} < x^*$ and $\bar{y_i} < y^*$.Similarly, it can be proven that when 2 $(\bar{x_i}, \bar{y_i})$ exist, $\bar{x_1} < \bar{x_2}$ and $\bar{y_2} < \bar{y_1}$.

Proof: In order for $(\bar{x_i}, \bar{y_i})$ to exist, the following two conditions must be met

$$r_1 + a_{11}\bar{x_i}^{b_{11}} + a_{12}\bar{y_i}^{b_{12}} = 1$$
$$r_2 + a_{21}\bar{x_i}^{b_{21}} + a_{22}\bar{y_i}^{b_{22}} = 1.$$

In order for $x*$ to exist, the following condition must be met

$$r_1 + a_{11}(x^*)^{b_{11}} = 1.$$

Similarly for y^*,

$$r_2 + a_{22}(y^*)^{b_{22}} = 1.$$

If $\bar{x_i} \geq x^*$, then $a_{12}\bar{y}^{b_{12}} \leq 0$, which cannot be true since all parameters are positive. If $\bar{x_i} = x^*$, then $a_{12}\bar{y_i}^{b_{12}} = 0$. Similarly, if $\bar{y_i} \geq y^*$, then $a_{21}\bar{x_i}^{b_{21}} \leq 0$, which cannot be true since all parameters are positive. Therefore, $\bar{x_i} < x^*$ and $\bar{y_i} < y^*$.■

Using these facts, a conjecture can be made about the stability of the equilibria. Conjecture 1: The stability of the equilibrium points has an alternating pattern described by these three cases.

Case 1: If no $(\bar{x}, \bar{y})$ exists, exactly one of $(x^*, 0)$ or $(0, y^*)$ is stable.

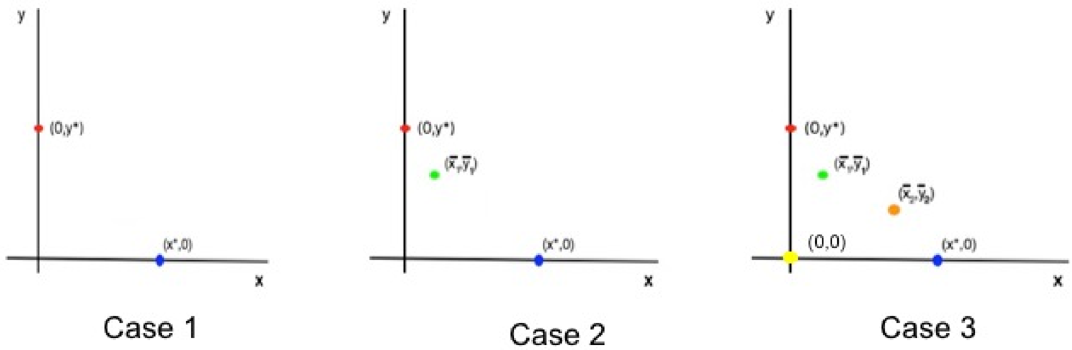

Figure 4: Cases for stability

Case 2: If one $(\bar{x}, \bar{y})$ exists, either $(\bar{x}, \bar{y})$ is stable and $(x^*, 0)$ and $(0, y^*)$ are unstable or $(x^*, 0)$ and $(0, y^*)$ are stable and $(\bar{x}, \bar{y})$ is unstable.

Case 3: If two $(\bar{x_i}, \bar{y_j})$ exists where $\bar{x_2} > \bar{x_1}$ and $\bar{y_1} > \bar{y_2}$, then either $(x^*, 0)$ and $(\bar{x_1}, \bar{y_1})$ are stable or $(y^*, 0)$ and $(\bar{x_2}, \bar{y_2})$ are stable.■

These cases can be seen easily through examples. Figure 5 shows an example of

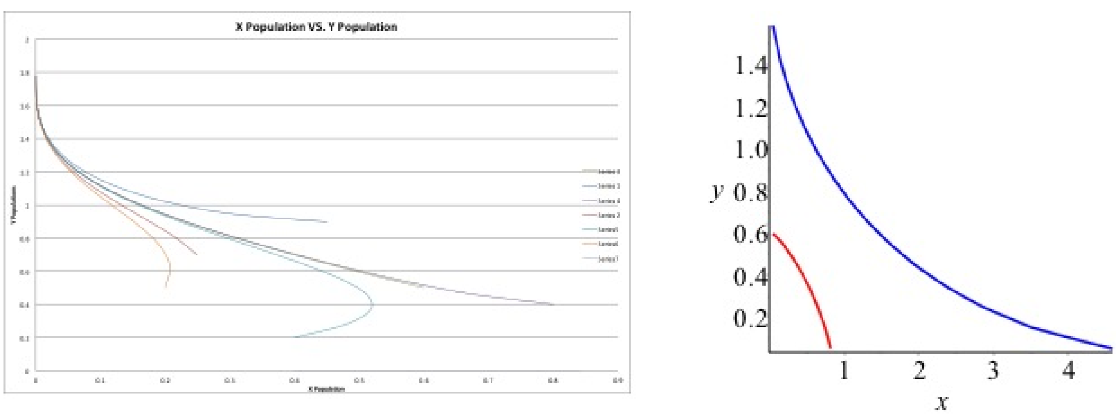

Figure 5: Case 1 Example

Case 1. There is no $(\bar{x}, \bar{y})$. Since the y population is more dominant, no matter the initial conditions, the populations always flow to $(0, y^*)$ no matter how close they get to $(x^*, 0)$. The isocurves of this example do not cross confirms that no $(\bar{x}, \bar{y})$ exists. Figure 6 shows an example of case 2. One $(\bar{x}, \bar{y})$ exists but it seems to be unstable. This $(\bar{x}, \bar{y})$ can be seen as the intersection in the isocurves. The populations flow to

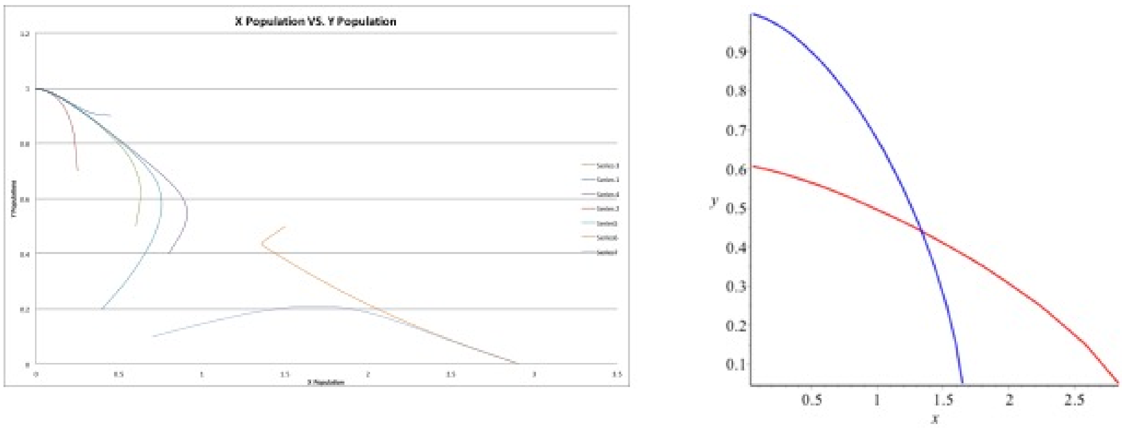

Figure 6: Case 2 Example

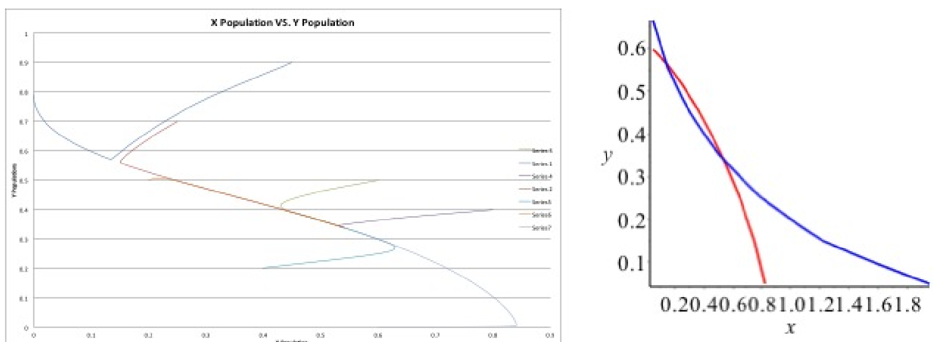

Figure 7: Case 3 Example

either $(x^*, 0)$ or $(0, y^*)$ depending on the initial condition. The boundary between these two basins of attraction need not be linear but if one population is drastically larger than the other, there is a high chance that it will dominate and the other population will take over. Figure 7 shows the example of Case 3. There are 2 intersections of the isocurves showing that 2 $(\bar{x_i}, \bar{y_i})$ exist. The populations only flow to the second coexistent equilibrium and $(0, y^*)$. One of the initial conditions leads to $(0, y^*)$ while the rest lead to the $(\bar{x_2}, \bar{y_2})$. The location of the unstable $(\bar{x_1}, \bar{y_1})$ is still important when looking at the boundary of the basins of attraction.

Conjecture 2: If an unstable $(\bar{x_i}, \bar{y_i})$ exists, it lies on the boundary between the basins of attraction. Figure 7 shows an example of this. The location of $(\bar{x_1}, \bar{y_1})$ is right where the two lines diverge to go to the two stable equilibria. This conjecture also applies when there is only one $(\bar{x}, \bar{y})$. This is shown in Figure 5. Therefore, as long as one unstable $(\bar{x_i}, \bar{y_i})$ exists, this conjecture applies.

Conjecture 3: The populations do not flow directly to the stable equilibria but rather to curve that flows to the equilibria. This trend has been seen in the examples created. As seen in Figures 5, 6, and 7, the populations do not flow directly to the stable equilibria but rather to curve that flows to the equilibria. This can be called the Equilibria Highway. The highway splits at the unstable equilibria but then continues afterwards. The form of this highway curve and the reason for it are of interest.

6 Differences between the Hassell-Comins Model and the New Model

As seen above, though both of these models have similar qualities, there are some important differences between the two models. One difference is the number of possible $(\bar{x_i}, \bar{y_i})$. The Hassell-Comins model had isoclines which could only intersect once while the new model has isocurves giving the opportunity for more than one intersection. This difference is important because having multiple coexistent equilibria to flow to may be more realistic than one coexistent equilibrium. If there are more stable equilibria, the initial conditions are more important. With only one stable equilibrium, the initial condition does not matter because the populations will always flow to that point.

The use of the isoclines/isocurves in these models are different. For the Hassell-Comins model, if the lines intersect, this means that a stable $(\bar{x}, \bar{y})$ exists. For this new model, though the isocurves may intersect more than once, this only means that the coexistent equilibria exist but they may not be stable. It is important to not confuse these two different uses of the isoclines/isocurves. The isocurves are still important since the location of the $(\bar{x}, \bar{y})$ cannot be easily found using non-numerical parameters.

Another difference in these models is the combinations of stable equilibria. In the Hassell-Comins model, if $(\bar{x}, \bar{y})$ was stable, then all populations would flow to it because neither x^* or y^* would be stable. This means that no matter the initial conditions, neither population would die off. The new model can have both a stable $(\bar{x_i}, \bar{y_i})$ and a stable x^* or y^* if there are more than one existing $(\bar{x_i}, \bar{y_i})$. The possibility of this combination makes the model seem more realistic in this sense. Though the only difference in these two models is the locations of the b parameters, this small change has impacted the model in some very important ways.

7 Future Research and Conclusions

While the nature of of the new model's equilibria have been explored and important differences in the models have been discovered, there is much more to be done to fully understand this new model. Though $(0, 0)$, $(x^*, 0)$, and $(0, y^*)$ have been explained in depth, there is much more to do in order to understand the coexistent equilibria. The location and stability of this point should be further developed. This exploration should take place because usually this type of equilibrium is desired.

Further work can also be done on the conjectures. In order to prove Conjecture 1, one must show when one equilibrium is stable, the adjacent ones are unstable. In order to prove this, the conditions for stability of $(\bar{x}, \bar{y})$ must be known. Proving that the unstable $(\bar{x}, \bar{y})$ equilibrium lies on the boundary between the basins of attraction will require solving for this boundary. Understanding this border can be very important in understanding this model because knowing this border can help control the environment.

Once this model is fully understood, finding species that fit this model would put this model to use. Finding trends that look similar to this model could then be used to predict future population trends. Once the model is used for certain populations, it can be used to help stabilize an environment that is struggling by leading the species into the right basin of attraction. The Leslie-Gowers model was able to be used with flour beetle populations. Because of this application, the Leslie-Gower method has left a big impact on the history of competition models. If our new models has applications, it will have great potential to also impact the history of competition models

Even though there is much more research to be done on this new model, many important parts of this model have been discovered showing that the continuation of research should be pursued. The conditions of stability for $(x^*, 0)$ and $(0, y^*)$ have been defined as well as the proof of the instability of $(0, 0)$. Many conjectures have been given on trends seen in this model. The differences in this model in comparison with the Hassell-Comins model are supportive in the importance of this model.

8 References

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