

A Game-theoretic Model of *Blepharisma* Population and Cannibalism Dynamics

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Abstract

Blepharisma are single-celled organisms that have the ability to consume other members of their species. Those that engage in cannibalism become giants, creating a distinct polymorphism of two possible states- either regular dwarf or cannibalistic giant. The exact conditions in the environment that give rise to this cannibalistic behaviour, in *blepharisma* and other cannibalistic species, has been the subject of some speculation and study. However, it has been suggested that a game-theoretic approach may be appropriate for determining when individuals may choose to engage in cannibalism. In this paper, a game-theoretic model of the dynamics of cannibalism within *Blepharisma* populations is created by incorporating best response dynamics into a discrete time population model. The model is used to test the effects of both total resource availability and population density on the prevalence of cannibalism, finding that increasing either of these environmental factors increases cannibalistic behaviour. It also reveals that cannibalism can have implications on total population size. Furthermore, it is possible, under certain conditions, for the modelled population to arrive at an equilibrium in which the entire population is either purely cannibalistic or non-cannibalistic rather than a coexistence of both states, and these conditions are mathematically solved for.

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Introduction:

Blepharisma are single-celled protists that are common subjects of scientific studies and instructional lab work in the field of ecology, due to their ability to ideally demonstrate major ideas in the theory of population dynamics. Important characteristics include their distinctive pink color due to the presence of the pigment Blepharismin which allows them to be easily recognized under a microscope, the ease of culturing populations of the species, reproduction by binary fission, and peculiar feeding behavior (Hanna, Bhandary, Giese 1973, NIES).

This feeding behavior in particular has been the subject of many inquiries and experiments. *Blepharisma* are able to consume any organism that is smaller than themselves, such as bacteria, algae, other protists, or even members of their own species. This cannibalistic behavior gives rise to an interesting polymorphism in the species. Cannibalism causes gigantism, and thus individuals that engage in cannibalism grow to approximately twice the size of those that don't (Polis). This allows for the prevalence of cannibalism to be experimentally observed in conjunction with resource levels and other environmental factors affecting the populations.

This intraspecific predation, whether in the context of *blepharisma* specifically or more generally across all species of nature in which it has observed, has given rise to questions regarding its purpose and cause. Because it accounts for such a significant portion of the mortality in many species in which it is manifested, it has been speculated that it may be a method of self-regulation of the population size (Polis, Cushing).

Furthermore, experiments have suggested that the prevalence of cannibalism is dependent upon the availability of resources and population density (Polis). There are two contrasting opinions regarding the effect of resources, however. One argues that cannibalism can be introduced and cause an equilibrium if resources are sufficiently high (Cushing), and the other contends that cannibalism arises in low resource environments, as once a bacterial food source becomes scarce, individuals will recognize that cannibalism is beneficial for survival. Cannibalism has been found to be density dependent (Polis), as having a high population density

will increase the rate of contact with other members of the species, further making cannibalism an easy method of feeding.

In terms of the offset of an individual's conversion to cannibalism, it is believed to be an adaptive, evolutionary decision based upon the benefits accrued to an individual. These benefits include those in the form of energy by having access to extra food, which translates to increased survival rates and reproductive success (Polis). Furthermore, it is assumed that individuals have a basic intuition in recognizing the environmental factors which indicate that adopting cannibalism may be beneficial. This individual, decision-making ability makes it possible to adopt a game theoretic perspective towards cannibal-dwarf interactions and the impact that this has on overall population dynamics. While cannibalism arises at the individual level, it is suspected that benefits on a population-wide level include the aforementioned purpose of self-regulation, as well as the possibility that cannibalism at low food levels may allow for continued survival of a population that would die out if it could not convert to cannibalism.

Thus, the model constructed in the following paper will hopefully serve to investigate these ideas and answer the question:

How do certain environmental factors, particularly resource availability and population density, affect the prevalence of cannibalism in *blepharisma* protists?

*Note: Throughout this paper, dwarves will be used to refer to regular-sized (non-cannibalistic) *blepharisma*, while the terms giant and cannibal will be used interchangeably to refer to those that do engage in cannibalism.

Purpose:

To introduce a mathematical model allowing for observation of *Blepharisma* population dynamics and dwarf-cannibal coexistence by incorporating a game-theoretic best response decision making process into a discrete time population model, and determine whether simulations with this model are consistent with predictions regarding the effects of resource level and population density on the prevalence of cannibalism.

Theoretical background to model:

As aforementioned, *Blepharisma* reproduce and sustain their populations by performing binary fission. Each individual of the species will have the opportunity to decide whether to engage in cannibalism and become a giant, or to remain a dwarf. The purpose of the model is to observe how this decision is dependent upon resource availability and how the dwarf-giant proportions affect the sustainability of the overall population. The model will operate using a discrete-time population update. At each of these times steps, individuals will take into account the resource availability and population density, and reconsider whether to remain a dwarf or become a giant. This decision will take the form of a best response dynamic, a common tool in evolutionary game theory for observing how members of a species adopt over time based on different “strategies” available to them and the “payoffs” in fitness associated with each strategy (Kleinberg, Ellison). The following summarizes the options available to each member of the population:

With a certain probability p_1 , which will be dependent upon the availability of resources, a dwarf will decide to consume an extra amount of resources which will enable them to grow such that they can choose one of the options of the best response dynamic, either to perform binary fission to produce two dwarves, or to become a giant. The decision will be made based on which of the two strategies, giant or dwarf, is more beneficial towards the individual’s fitness at that particular time. If a dwarf decides not to go into the best response at a given time step they will simply remain a dwarf.

The options available to giants are slightly more complex. First of all, it should be mentioned that as long as their diet remains consistent, cannibal giants will divide to produce more giants, but if sufficiently large prey become unavailable the offspring will revert to normal size (Giese 1938). Based on this, at each time step a giant will be given the chance to split into two giants, and this decision will be resource-dependent and occur with probability p_2 . Like dwarves, giants can go into the best response dynamic; where they either split into two dwarves or remain a giant. However, since neither of these choices are resource dependent (neither

requires consumption of sufficient extra resources), this will occur at a fixed probability, q . If a giant decides neither to split into two giants nor enter the best response at a given time step, they will simply remain a giant.

Assumptions:

Several assumptions are made regarding the nature of blepharisma and the nature of their environment for the purposes of this model. Firstly, it is assumed that blepharisma are able to obtain information regarding the availability of resources as well as population density in order to make their decision. Studies do suggest that this is true to some extent, and blepharisma are able to gauge approximate resource and population levels based upon their current diet and contact with others (Polis, Cushing). Furthermore, as with other applications of game theory, it is assumed the players, in this case the blepharisma, are perfectly rational beings that always make the most beneficial decision, and that they are acting exclusively for their own interests. For the purposes of this model it is also assumed that total bacterial resource levels are constant, and that the entire system of blepharisma populations and resource levels is closed and free from outside interference.

Model Construction

Parameters and Variables:

n = dwarf population

N = giant population

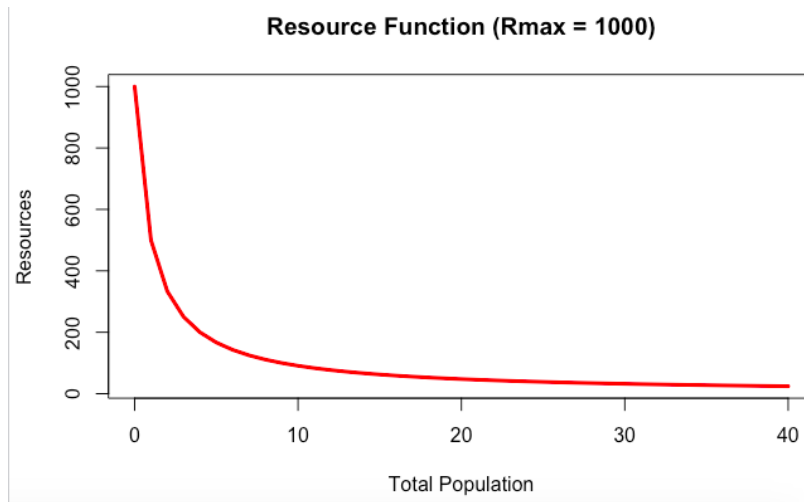
t = timestep

Δt = length of one timestep (small).

$R(n,N)=\frac{R_{max}}{1+n+N}$. This resource function quantifies the availability of resources for each

individual. R_{max} is the total available resources and can be thought of as the total number of bacteria living amongst the blepharisma and assumed to remain constant by this model. As the total population increases, the availability for each individual decreases, thus this appears as a

decaying inverse function. The 1 in the denominator serves to prevent the function from becoming undefined when the total population is 0.



a = rate at which a giant encounters and consumes dwarfs

q = rate at which giant enters the best response dynamic

d = constant mortality rate (probability of any individual dying of natural causes during a timestep).

Resource-dependent probabilities:

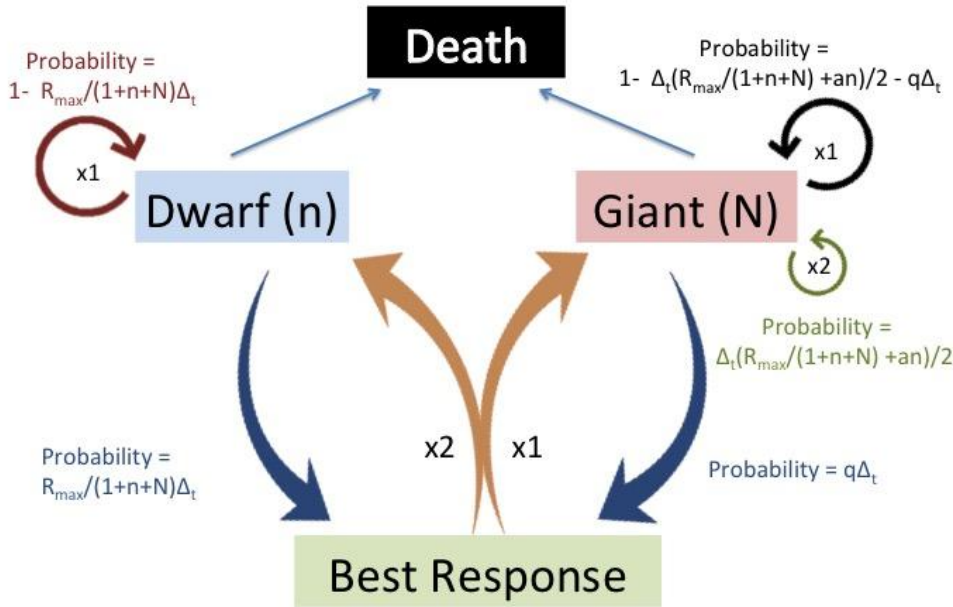
For dwarfs, $p_1 = R/(n+N)$. Since dwarves can only consume bacteria, this probability is equal to the resource function.

For giants $p_2 = (R/(n+N) + an)/2$. Because giants are able to consume bacteria and also have the alternative nutrient source of consuming dwarves, the resource function is added to the expected number of dwarves they can eat. Furthermore, there is an extra cost of resources associated with being a giant, due to the increased size. Since a giant is approximately twice the size of a dwarf, this extra necessity in diet justifies the division by 2 in the probability.

Payoffs: These quantify the expected benefit in fitness for each strategy at any given time by incorporating both resources and the probability of dying to give what is effectively a per-capita growth rate.

Dwarf: $s_1 = 2p_1 - d - aN$

Giant: $s_2 = 2p_2 - d$



Discrete-time population update equations:

The following are the discrete time population equations that essentially comprise the entire model. Each gives the population of blepharisma playing each strategy in the next time step, based upon the events that occurred and decisions made in the previous.

Dwarf:

$$\underbrace{n_{t+1}}_{\text{Dwarf population in next time step}} = \underbrace{n_t(1 - p_1\Delta_t)}_{\text{All that chose not to enter best response}} + \left\{ \begin{array}{ll} 2(n_t p_1 \Delta_t + N_t q \Delta_t) & \text{if } s_1 > s_2 \\ 0 & \text{if } s_1 < s_2 \\ \frac{n_t p_1 \Delta_t + N_t q \Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - \underbrace{dn_t \Delta_t}_{\text{Deaths}} - \underbrace{aN_t n_t \Delta_t}_{\text{Those that are cannibalized}}$$

Giant:

$$\begin{aligned}
\underbrace{N_{t+1}}_{\text{Giant population in next time step}} &= \underbrace{2N_t(p_2\Delta_t)}_{\text{2 for all that split}} + \underbrace{N_t(1 - p_2\Delta_t - q\Delta_t)}_{\text{All that chose to neither split nor enter best response}} + \left\{ \begin{array}{ll} 0 & \text{if } s_1 > s_2 \\ \frac{n_t p_1 \Delta_t + N_t q \Delta_t}{2} & \text{if } s_1 < s_2 \\ \frac{n_t p_1 \Delta_t + N_t q \Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - \underbrace{dN_t\Delta_t}_{\text{Deaths}}
\end{aligned}$$

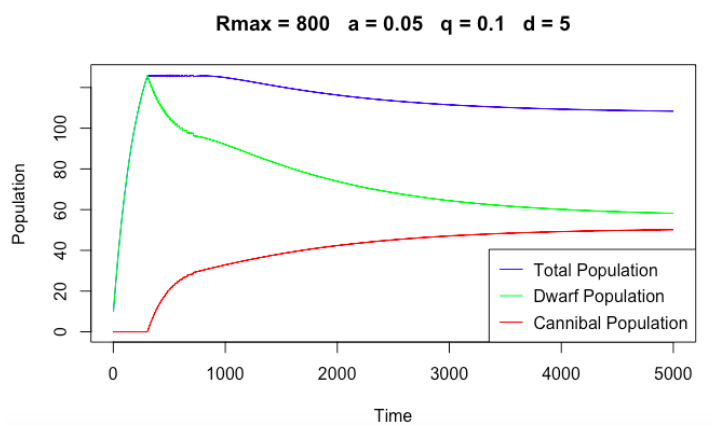
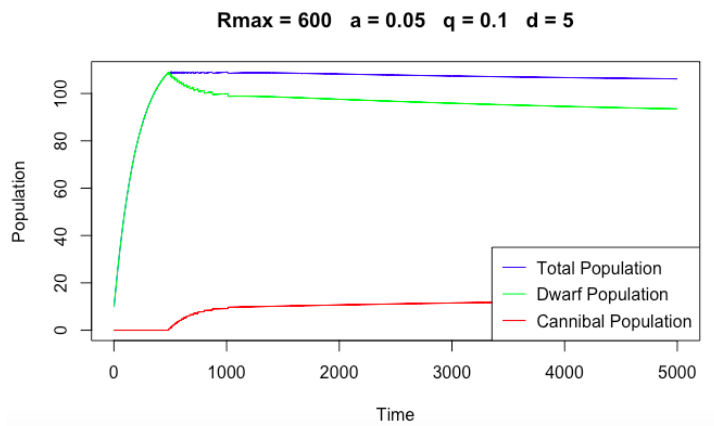
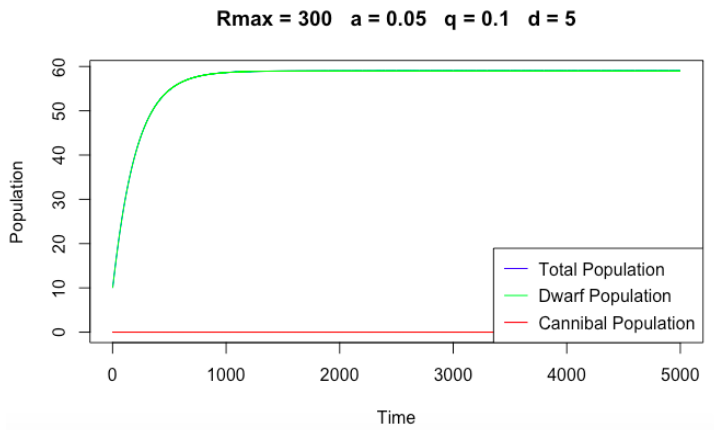
Within the brackets are the three scenarios of the best response dynamic. $n_t p_1 \Delta_t$ is the number of dwarfs that entered the best response, and $N_t q \Delta_t$ is the number of giants that did so. If dwarf is the better payoff, 2 dwarfs will be added for each blepharisma that went into the best response since they will have all split into two dwarves, and there will be no addition to the giant population. Similarly, if giant was the better payoff, all blepharisma that entered the best response will be giants in the next time step and nothing will be added to the dwarf population.

It should be noted that Δ_t serves a dual purpose when it is multiplied with all variables that are intended to be probabilities in the above equations (p_1 , p_2 , a , q , and d). In addition, as defined in the simulations, these values are not necessarily in probabilistic form (they are not necessarily less than 1), as both p functions depend on the resource function and a , q , and d are expressed as integer rates. Because Δ_t is some arbitrarily small number, it scales these values down to small, probabilistic numbers while preserving the relative proportion between p_1 and p_2 and converts rates to numbers of blepharisma.

Basic Model Behavior:

The model was created into an R code (Appendix A) in order to enable visualization of long-term simulations. The following graphs depict some behaviors of this model and its response to alterations in various parameters, with the starting population conditions being set to 10 dwarves and no cannibals:

Effect of increasing Rmax



When R_{\max} is set to a sufficiently low level, such as in the case of the first graph when it

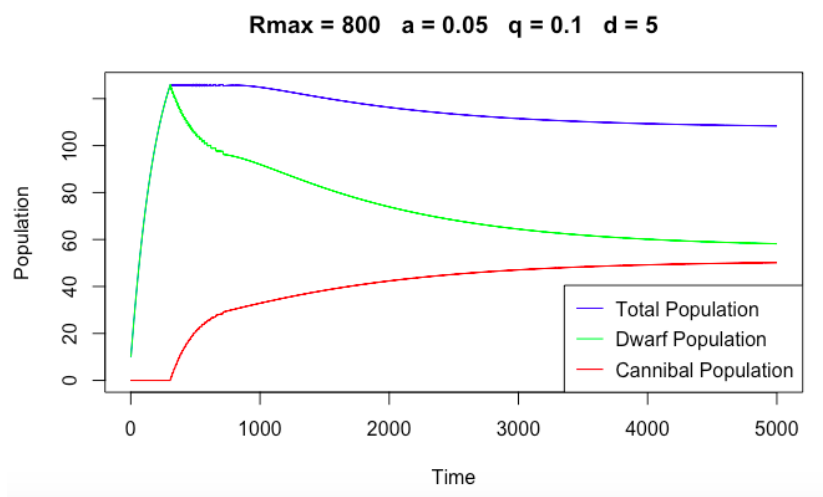
is at 300, the population will remain at a pure dwarf equilibrium, quickly growing until stabilization at a carrying capacity.

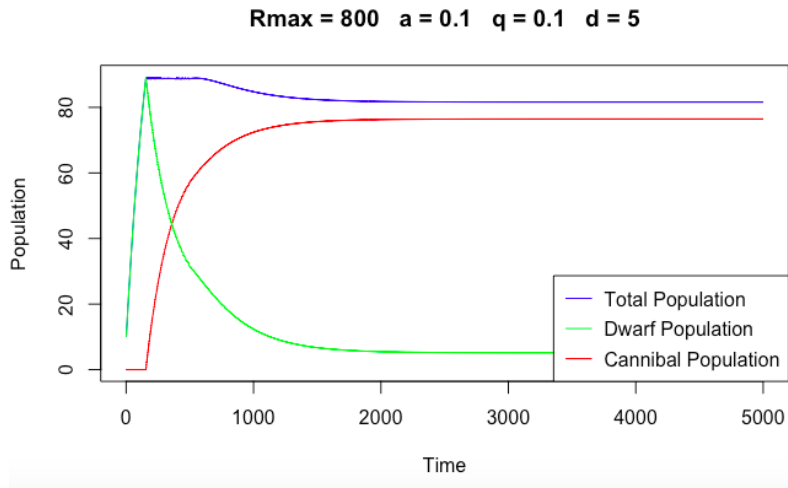
When we double R_{\max} to 600 in the second graph, we will again see a rapid growth of the dwarf population to a level higher than previously. However, at a certain point cannibalism will become worthwhile, and some giants will be introduced to the population. This will cause a slight decrease in the dwarf population, and both will stabilize to give a mixed giant-dwarf equilibrium.

When we increase R_{\max} further to 800 as in the 3rd graph, we again see dwarf growth to an even higher maximum, before a giant influx. However, this giant influx is much higher, causing the dwarf decrease to be higher as well, and the two populations seem to converge to a similar level.

Intuitively, the total population (represented by the blue line) reaches a higher level with each increase in the abundance of resources. However, in the 3rd scenario, the giant influx appears to cause a slight dip in this total population. This suggests that while switching to giant becomes prudent for certain individuals in the population, it may be detrimental to the population as a whole, which is consistent with a prediction made by Polis.

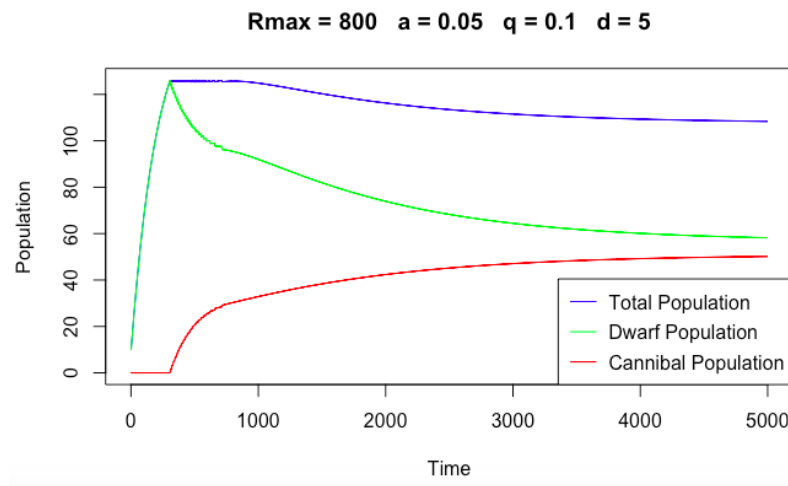
Effect of increasing a

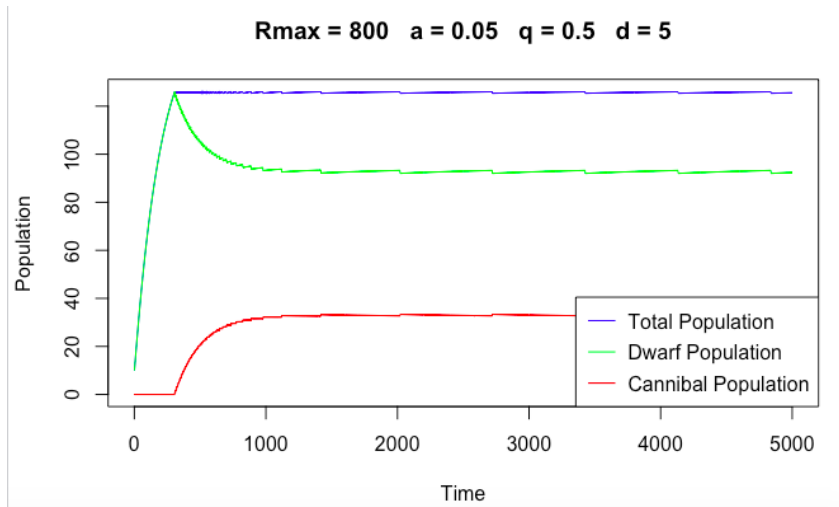




If we take the settings from the 3rd graph in the previous analysis and, keeping all the other parameters the same, double a , we will notice a domination of cannibals. This is akin to a doubling in the population density. Obviously, increasing the convenience with which dwarves can be encountered and consumed significantly increases the payoff of being a giant, and causes more dwarves to switch. This, however, damages the overall population size.

Effect of increasing q





If we double q , the rate at which giants enter the best response dynamic, instead of a , we observe the above change in the behaviour of the simulation. Rather than converging to a similar population size, the dwarf and giant populations become stable and reach equilibrium at a much earlier time stage, leaving a large gap between the two population sizes. The likely reason for this is simply that this increases the rate of switching between populations, causing a faster equilibration.

Model Analysis

This section will concern itself with seeking more rigorous analyses of the nature of the model, particularly in regards to stability conditions and equilibria.

Continuous Equations and Phase Plane

A very useful qualitative tool in visualizing the behaviour and stability of nonlinear systems, including predator-prey models such as this, is a phase plane (Dawkins, Jeng, Tseng). When a model involving a pair of variables is expressed with differential equations describing their evolution over time and its dependence upon the other variable, phase planes can map

trajectories of the solutions of the equations to display the dynamics in the relationship between the two variables and points at which stability occurs.

In order to accomplish this, we must convert our discrete-time equations into continuous differential equations.

$$n_{t+1} = n_t(1 - p_1\Delta_t) + \left\{ \begin{array}{ll} 2(n_t p_1\Delta_t + N_t q\Delta_t) & \text{if } s_1 > s_2 \\ 0 & \text{if } s_1 < s_2 \\ \frac{n_t p_1\Delta_t + N_t q\Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dn_t\Delta_t - aN_t n_t\Delta_t$$

Distribute \uparrow This n_t term

$$n_{t+1} = n_t - n_t p_1\Delta_t + \left\{ \begin{array}{ll} 2(n_t p_1\Delta_t + N_t q\Delta_t) & \text{if } s_1 > s_2 \\ 0 & \text{if } s_1 < s_2 \\ \frac{n_t p_1\Delta_t + N_t q\Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dn_t\Delta_t - aN_t n_t\Delta_t$$

If we subtract n_t , we get an expression for the growth in population from n_t to n_{t+1}

$$n_{t+1} - n_t = -n_t p_1\Delta_t + \left\{ \begin{array}{ll} 2(n_t p_1\Delta_t + N_t q\Delta_t) & \text{if } s_1 > s_2 \\ 0 & \text{if } s_1 < s_2 \\ \frac{n_t p_1\Delta_t + N_t q\Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dn_t\Delta_t - aN_t n_t\Delta_t$$

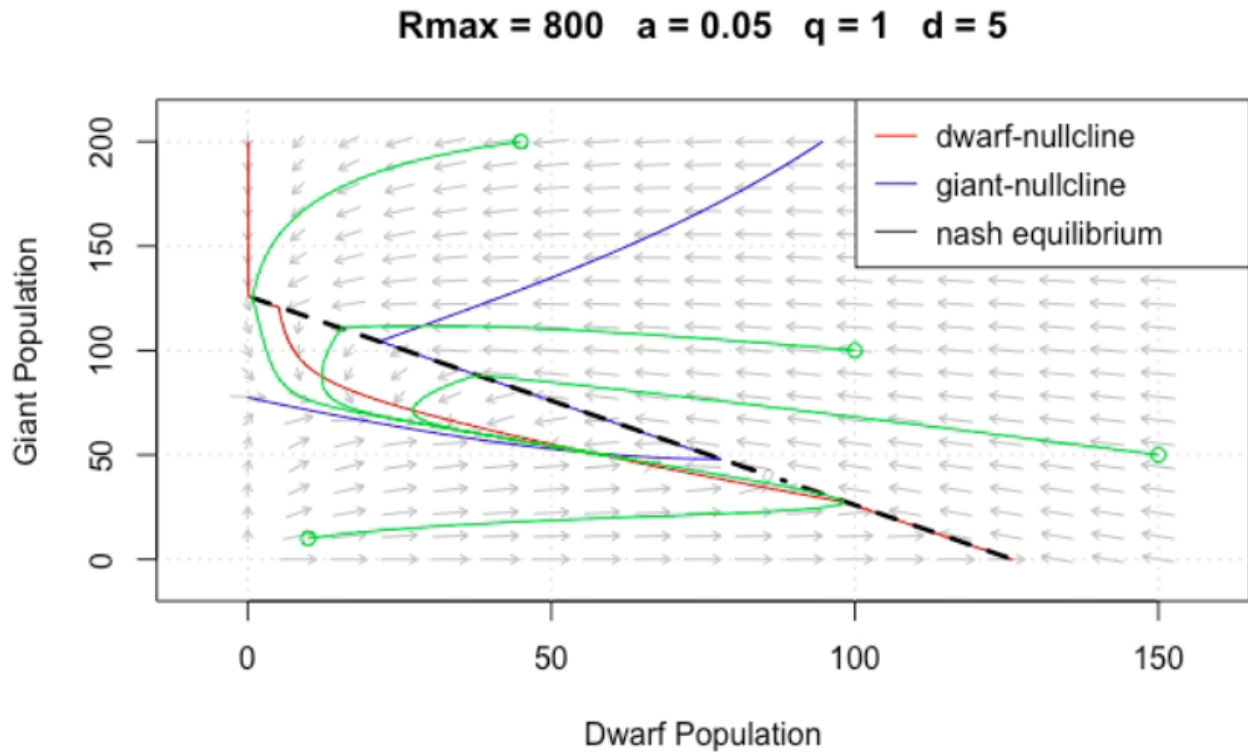
If we divide by Δ_t , the expression becomes for this growth per time, or the derivative.

$$\frac{dn}{dt} = -n_t p_1 + \left\{ \begin{array}{ll} 2(n_t p_1 + N_t q) & \text{if } s_1 > s_2 \\ 0 & \text{if } s_1 < s_2 \\ \frac{n_t p_1 + N_t q}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dn_t - aN_t n_t$$

We can follow the same steps for the giant population equation:

$$\begin{aligned}
N_{t+1} &= 2N_t(p_2\Delta_t) + N_t(1 - p_2\Delta_t - q\Delta_t) + \left\{ \begin{array}{ll} 0 & \text{if } s_1 > s_2 \\ n_t p_1 \Delta_t + N_t q \Delta_t & \text{if } s_1 < s_2 \\ \frac{n_t p_1 \Delta_t + N_t q \Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dN_t \Delta_t \\
N_{t+1} &= 2N_t p_2 \Delta_t + N_t - N_t p_2 \Delta_t - N_t q \Delta_t + \left\{ \begin{array}{ll} 0 & \text{if } s_1 > s_2 \\ n_t p_1 \Delta_t + N_t q \Delta_t & \text{if } s_1 < s_2 \\ \frac{n_t p_1 \Delta_t + N_t q \Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dN_t \Delta_t \\
N_{t+1} - N_t &= N_t p_2 \Delta_t - N_t q \Delta_t + \left\{ \begin{array}{ll} 0 & \text{if } s_1 > s_2 \\ n_t p_1 \Delta_t + N_t q \Delta_t & \text{if } s_1 < s_2 \\ \frac{n_t p_1 \Delta_t + N_t q \Delta_t}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dN_t \Delta_t \\
\frac{dN}{dt} &= N_t p_2 - N_t q + \left\{ \begin{array}{ll} 0 & \text{if } s_1 > s_2 \\ n_t p_1 + N_t q & \text{if } s_1 < s_2 \\ \frac{n_t p_1 + N_t q}{2} & \text{if } s_1 = s_2 \end{array} \right\} - dN_t
\end{aligned}$$

Using the PhaseR package and the code in Appendix B, the phase plane can be constructed for the following particular parameter settings:



The nullclines represent the lines on which the respective differential equations are equal to 0. Thus, on the dwarf nullcline, the dwarf population is not changing, and likewise on the giant nullcline (these lines are jagged due to the piecewise-defined nature of the differential equations). The dashed black line represents points which are Nash equilibria, at which the payoffs are equal. The green lines are various trajectories, with the circles being the starting positions (starting dwarf and giant populations).

It is evident that regardless of the starting populations, all trajectories lead to the single point at which the dwarf and giant nullclines intersect, and thus neither population is changing. Although this is logical, what is surprising is that this point is not also a Nash equilibrium, and the payoffs are not equal.

Pure equilibria:

The phase plane analysis demonstrates that for particular parameter settings that allow for a mixed giant-dwarf equilibrium, this equilibrium will always arrive at the same population sizes regardless of the starting sizes. It is also possible to solve for the cases of pure equilibrium- when only either dwarfs or giants will exist.

Let us begin by investigating what conditions are necessary for there to be a purely dwarf equilibrium. We can assume that at this point, the giant population, N , will be 0. In addition, at stability, the dwarf population will not be changing. Therefore, n_{t+1} will be equal to n_t , and we can set these two values to be equal in our dwarf discrete-time equation. Let us do so, and denote this stable dwarf population to be n^* .

$$n^* = n^*(1 - p_1\Delta t) + \begin{cases} 2(n^* p_1\Delta t) & \text{if } s_1 > s_2 \\ 0 & \text{if } s_1 < s_2 \\ n^* p_1\Delta t / 2 & \text{if } s_1 = s_2 \end{cases} - dn^*\Delta t$$

Again, all terms that had N are removed, because we know N must be 0.

Still, the piecewise section appears to be creating complications, however with further thought it is evident that only one of the options must be true. In order for this pure dwarf equilibrium to be stable, we need the dwarf payoff to be greater than the giant one, otherwise some dwarfs would simply switch to giants in the next time step. Therefore, it must be true that $s_1 > s_2$, and we can take the corresponding term of the piecewise to leave an equation that can be easily solved for n^* .

$$n^* = n^*(1 - p_1 \Delta t) + 2n^* p_1 \Delta t - dn^* \Delta t$$

$$n^* = n^* - n^* p_1 \Delta t + 2n^* p_1 \Delta t - dn^* \Delta t$$

$$0 = n^* p_1 \Delta t - dn^* \Delta t$$

$$0 = n^* (p_1 - d)$$

So either $n^* = 0$, or $p_1 = d$

If $p_1 = d$, then since $p_1 = R(n^*, 0) = \frac{R_{\max}}{1 + n^*}$,

$$\frac{R_{\max}}{1 + n^*} = d$$

$$1 + n^* = \frac{R_{\max}}{d}$$

$$n^* = \frac{R_{\max}}{d} - 1$$

So, we've solved that a stable dwarf equilibrium can occur when n is either 0, or $\frac{R_{\max}}{d} - 1$

Obviously, if n is 0 when N is also 0, then this is the equilibrium at which the entire population will remain at 0, as there will be no blepharisma present to continue the population. The latter is the more interesting situation, as it reveals that if the number of dwarfs present is equal to $(R_{\max}/d) - 1$ and there are no cannibals present, a pure dwarf equilibrium will exist. Now, in order to guarantee that the dwarf population will remain at that level and none will switch to giant, we must make sure that the condition $s_1 > s_2$ will also be satisfied, which must mean that

$$R(n,0) > \frac{R(n,0) + an}{2}$$

$$2R(n,0) > R(n,0) + an$$

$$R(n,0) > an$$

$$\frac{R_{\max}}{1+n} > an$$

Thus, this implies that so long as the resource function is greater than the number of dwarves a cannibal would be expected to consume, the dwarf equilibrium will remain stable. This is logical, as there is no expected improvement in the availability of food that isn't outweighed by the additional cost in resources associated with becoming a giant.

We can follow the same process to solve for the conditions necessary for a pure giant equilibrium to exist. First we assume $n=0$ and find the N^* such that the giant population is not changing, while also assuming that $s_2 > s_1$ is the true piecewise subfunction to ensure that giants will not switch to dwarf:

$$N^* = 2N^*p_2\Delta t + N^*(1 - p_2\Delta t - q\Delta t) + N^*q\Delta t - dN^*\Delta t$$

$$N^* = 2N^*p_2\Delta t + N^* - N^*p_2\Delta t - N^*q\Delta t + N^*q\Delta t - dN^*\Delta t$$

$$0 = N^*p_2\Delta t - dN^*\Delta t$$

$$0 = N^*(p_2 - d)$$

$$N^* = 0 \text{ or } p_2 = d$$

Again, $N^*=0$ will result in the same situation of the entire population being extinct that we saw before. So, we're only interested in $p_2=d$:

$$p_2 = d$$

$$\frac{1}{2} \left(\frac{R \max}{1 + N^*} \right) = d$$

$$\frac{R \max}{1 + N^*} = 2d$$

$$N^* = \frac{R \max}{2d} - 1$$

This is very similar to the condition seen with the dwarf equilibrium, apart from the d being replaced by $2d$. Now, we check when $s_2 > s_1$:

$$s_2 > s_1$$

$$2p_2 - d > 2p_1 - d - aN$$

$$2 \left(\frac{1}{2} \right) \left(\frac{R \max}{1 + N} \right) > 2 \left(\frac{R \max}{1 + N} \right) - aN$$

$$\left(\frac{R \max}{1 + N} \right) < aN$$

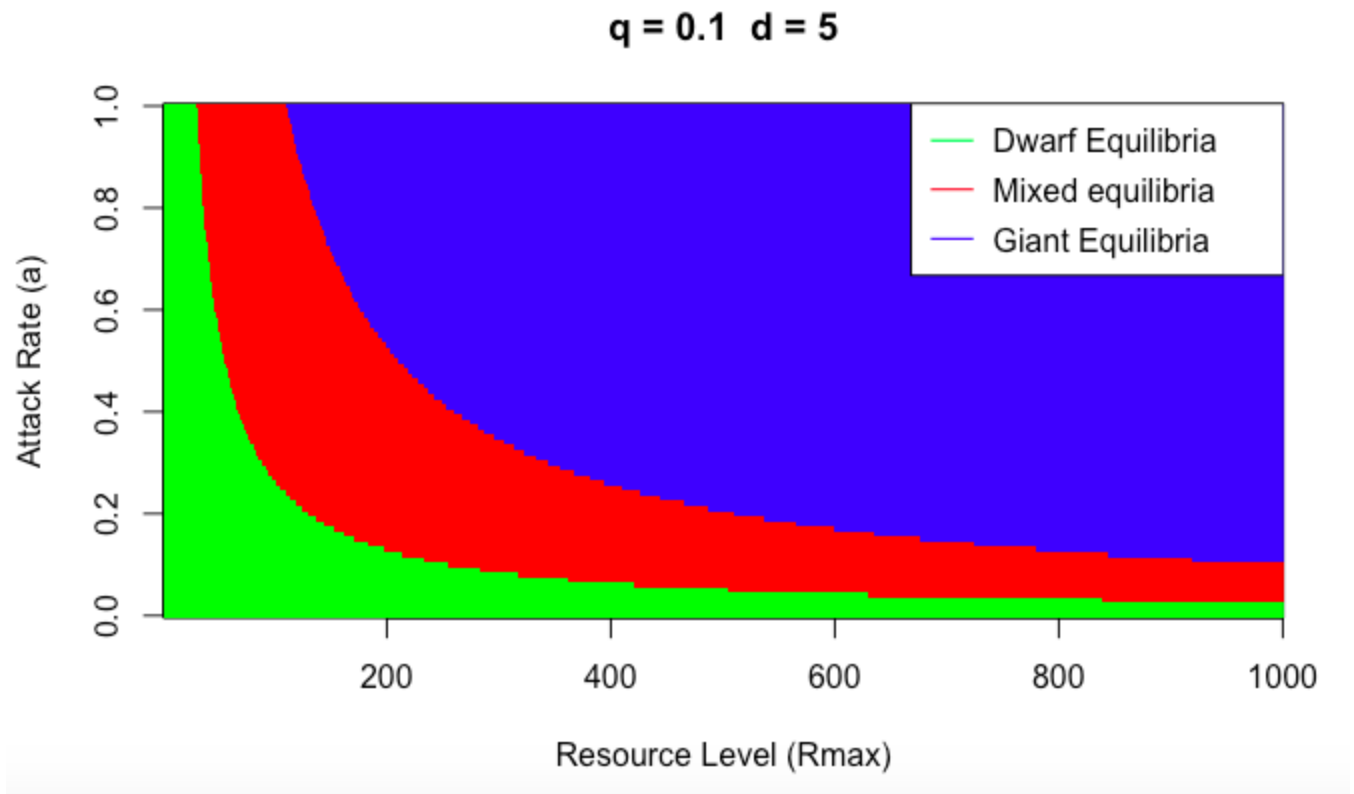
Again, this is similar to the condition necessary for the pure dwarf equilibrium. In this case, the threat of being cannibalized must be sufficiently large that individuals will not switch to dwarf.

And thusly, we have established the conditions necessary for either a stable dwarf or giant equilibrium to exist.

Stability Analysis:

Another R code (Appendix C) was written to visualize how the type of equilibrium that is

reached is dependent upon the parameter values defined. In particular, R_{max} and a seem to be the most influential on determining whether a pure dwarf, pure giant, or mixed equilibrium will occur. Therefore, this code was designed to test a matrix of various combinations of R_{max} and a and test whether the population would arrive at an equilibrium with only dwarves, only giants, or both. The range of R_{max} values tested is plotted on the x-axis, the same for a is on the y-axis, and the point corresponding to each combination is colored depending on the type of equilibrium.



It can be seen from the graph that if either parameter is sufficiently low, only dwarves will exist, and if either is sufficiently high, cannibalism will dominate, with a band of combinations in between for which the equilibrium will contain both. This appears to prove that both increasing resource abundance and population density each increase the prevalence of cannibalism.

Discussion and Conclusions:

Predictions of Model

The observed behaviour of the model can now be used to address some of the questions posed in the introduction based on studies in literature.

The first was the discussion of whether cannibalism would be more prevalent in high or low resource environments. Based upon the observations in the “Increasing R_{\max} ” section of the basic model behavior and the stability analysis, it appeared that cannibalism dominated when the number of resources available were high. Thus, this appears to be the condition most conducive to an increasing proportion of cannibalism in the overall population as this model predicts.

However, there was also the suggestion that if resource levels become extremely low, then cannibalism could allow a species to continue to exist by enabling some members to consume others and survive when they would otherwise all starve. This particular theory was not investigated in this paper, but in order to do so the population of this model in highly limited resource environments could be compared to that of a basic model in which cannibalism is not an option.

The model did accurately show that the frequency of cannibalism would increase as the population density, which was simulated by the contact rate, a , increased. Based upon the rate that they are coming into contact with other *blepharisma*, an individual would have a general sense of the population density within their environment. Subsequently, as a higher rate of contact with others gives more potential victims if one were to become a cannibal, the predicted payoff of becoming a giant increases and more dwarves will switch.

Beyond these specific predictions, the model showed that in general, different conditions would result in the population being either pure dwarves or pure cannibals, and only in few select conditions would there be a mixed equilibrium. When mixed equilibrium can exist, the phase plane analysis reveals that the stability will always occur at the same dwarf and giant population levels for a given set of parameter values regardless of the starting populations.

Future Directions

There are several routes through which the dynamics of the model can be further extended and observed beyond the scope of this paper. For example, although the model was used to test some general predictions made in literature regarding the prevalence of cannibalism in *Blepharisma* populations in nature and how it is affected by resource fluctuations and population density, specific quantitative data from experiments conducted to investigate these effects with which to compare model behavior were not found. If such data is available and could

be found, it would make possible for the model to be more rigorously compared to the true dynamics that it seeks to imitate.

There was a peculiarity observed in the phase plane analysis in regards to the point at which the dwarf and giant population nullclines intersected, which indicated the population levels that would always be reached in a mixed equilibrium. This point did not lie on the line indicating nash equilibria, where the payoffs for the two strategies are equal. The answer to why this is the case remains elusive and would require a more analytical solution of the conditions of the mixed equilibria.

Other possible alterations can be made to the assumptions and construction of the model itself in order to make it more robust and perhaps more reflective of nature. For example, rather than having the mortality rate be constant, it could vary depending on factors that would actually affect it in nature, such as being an inverse function of resource levels. Another assumption of the model was that blepharisma would always choose the more beneficial option of the best response dynamic. While it is accepted that they do have a general intuition regarding which would be best, they would likely not necessarily make the “right” decision every time in nature. Thus, the model could incorporate a chance of error, or a percentage of blepharisma in each time step that make the wrong decision in the best response.

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Appendices:

Appendix A: Model Simulation Code

```
# blepharisma_model(a = 0.05,q = .1,n0 = 10,N0 = 0,dt = .001, Rmax = 800, d = 5, T = 5000)
blepharisma_model = function(a, q, n0, N0, dt, Rmax,d, T = 5000){
  dat = matrix(0, T, 6)
  dat[1,1] = n0
  dat[1,2] = N0
  q = q*dt
  for(t in 1:(T-1)){
    n = dat[t,1]
    N = dat[t,2]
    p1 = (Res(n,N,Rmax))*dt#Dwarf Prob
    p2 = ((Res(n,N,Rmax))+a*n)/2*dt #Giant Prob
    d_pay = 2*p1 - d*dt - a*N*dt
    g_pay = 2*p2 - d*dt
    dat[t+1,1] = n*(1-p1) + 2*(p1*n + q*N)*(d_pay > g_pay) + (p1*n + q*N)/2*(d_pay == g_pay) -
d*n*dt - a*n*N*dt
    dat[t+1,2] = 2*N*p2 + N*(1-q-p2) + (p1*n + q*N)*(d_pay < g_pay) + (p1*n + q*N)/2*(d_pay ==
g_pay) - d*N*dt
    dat[t,4] = d_pay
    dat[t,5] = g_pay

  }
  dat[,3] = dat[,1] + dat[,2]
  plot(dat[,3], type = "l", col = "blue", main = "Rmax = 800 a = 0.05 q = 0.1 d = 10", ylim
= c(0, max(dat[,])),xlab = "Time",ylab = "Population")
  lines(dat[,2], col = "red")
  lines(dat[,1],col = "green")
  dat
}

Res = function(n,N,R){
  R/(1 + n + N)
}
```

Appendix B: Phase Plane Code

```
#Try: ODE_solve(800,.05,.1,5)
#Or Try: phase_plane(800,.05,.1,5)
params = c(0,0,0,0)
```

```

n_derivative = function(t,y,parameters){
  n = y[1]
  N = y[2]

  Rmax = parameters[1]
  a = parameters[2]
  q = parameters[3]
  d = parameters[4]

  p1 = Rmax/(1+n+N)
  p2 = (Rmax/(1+n+N) + a*n)/2
  dy = numeric(2)
  d_pay = 2*p1 - d - a*N
  g_pay = 2*p2 - d
  dy[1] = -p1*n + 2*(p1*n + q*N)*(d_pay > g_pay) - d*n - a*n*N
  dy[2] = N*p2 - N*q + (p1*n + q*N)*(g_pay > d_pay) - d*N

  list(dy)
}

fitness_difference = function(n,N){
  Rmax = params[1]
  a = params[2]
  q = params[3]
  d = params[4]

  p1 = Rmax/(1+n+N)
  p2 = (Rmax/(1+n+N) + a*n)/2
  dy = numeric(2)
  d_pay = 2*p1 - d - a*N
  g_pay = 2*p2 - d
  d_pay - g_pay
}

phase_plane = function(Rmax, a, q, d){
  blepharisma.flowField <- flowField(n_derivative, x.lim = c(0, 200), y.lim = c(0, 200),
  parameters = c(Rmax, a, q, d), points = 19, add = FALSE)
  grid()
  blepharisma.nullclines <- nullclines(n_derivative, x.lim = c(0, 200), y.lim = c(0, 200),
  parameters = c(Rmax, a, q, d), points = 500)
  y0 <- matrix(c(150, 150, 150, 100,45,200), ncol = 2, nrow = 3, byrow = TRUE)
  blepharisma.trajectory <- trajectory(n_derivative, y0 = y0, t.end = 10, parameters = c(Rmax,
  a, q, d), colour = rep("green", 3))
  params <- c(Rmax, a, q, d)
  contour(x = 1:200, y = 1:200, z = outer(1:200,1:200,fitness_difference), levels = c(0), add
  = TRUE)
  legend("bottomright", col = c("red", "blue"), legend = c("x-nullcline", "y-nullcline"), lty
  = 1)
}

```

```

ODE_solve = function(Rmax, a, q, d){
  blepharisma.numericalSolution <- numericalSolution(n_derivative, y0 = c(10, 0), t.end = 5,
type = "one",parameters = c(Rmax,a,q,d), colour = c("green", "orange"),xlab = "time", ylab =
"Population", ylim = c(0, 150))
  legend("bottomright", col = c("green", "orange"), legend = c("dwarfs", "giants"), lty = 1,
text.width = .8)

}

```

Appendix C: Stability Analysis Code

```

params = c(0,0)

is_stable = function(Rmax,a){

  q = params[1]
  d = params[2]

  n_star = Rmax/d-1
  N_star = Rmax/(2*d) - 1

  nstar_d_pay = 2*Rmax/(1+n_star) - d
  nstar_g_pay = (Rmax/(1+n_star) + a*n_star) - d

  Nstar_d_pay = 2*Rmax/(1+N_star) - d - a*N_star
  Nstar_g_pay = Rmax/(1+N_star) - d

  1*(nstar_d_pay > nstar_g_pay) + 2*(Nstar_d_pay < Nstar_g_pay)
}

sample_stability = function(q,d){
  params <- c(q,d)
  image(1:1000, (0:100)/100 ,outer(1:1000, (0:100)/100, is_stable), ylab = "Attack Rate", xlab
= "Resource Level", col = rainbow(3))
  legend("topright", col = c("green","red","blue"), legend = c("Dwarf Equilibria", "No
single-strategy equilibria", "Giant Equilibria"), lty = 1, text.width = 400, y.intersp = 2)
}

```

