Density Games

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I. Aim of the paper

This paper focuses on improving the limitations of standard replicator equations in modelling evolutionary dynamics of species playing games in a densely / sparsely packed environments. By redefining the replicator equation in a logistic form, the effect of population density brings in the dependence of growth rates in determining the stability of our coexisting equilibrium in 2D systems. The authors have exactly solved a 2 species game and analysed the stability of its equilibrium points. Our density equation also predicts limit cycles that can occur in certain cases of payoffs and growth rates. These properties were not an outcome of the standard replicator equations.

II. What did I do? Analytical Derivations and numerical results

A. Analysis of Monomorphic equilibrium and equivalence with replicator equation

We follow the equations defined in Appendix-A. Monomorphic equilibrium is a case where only one species dominates and survives the game after a long time. Let this species be i. Then, $y_i = 1$ and $y_j = 0\ \forall j \neq i$. Our claim says that in replicator and in density, equilibrium demands,

$$f_i = \bar{f} = \sum_{i,j} a_{ij} y_i y_j = a_{ii}, K_i = \sum_j a_{ij} y_j = a_{ii} = x_T \tag{1}$$

Therefore, we get the fact that the carrying capacity, which by definition is the payoff of ith species must equal the total population of our species i. So we see that if $y_i = 1$ for only one i in our density equation, then that means we have its payoff equal to average payoff as in the replicator equation.

Stability analysis about the monomorphic equilibrium gives the eigenvalues as:

$$e_j = \begin{cases} -r_i & \text{if } j = i \\ -r_j \left(\frac{a_{ii}}{a_{ji}} - 1\right) & \text{if } j \neq i \end{cases}$$

So, in order to be stable we only need to ensure that $a_{ii} > a_{ji}\ \forall i \neq j$. This is the exact same condition for a strategy to be evolutionarily stable [1] . Thus, even the stability of monomorphic equilibrium is identical to those of replicator. The same can also be seen in Fig. 1(a),(b). This concludes our analysis on the monomprphic equilibrium in our 2D density system.

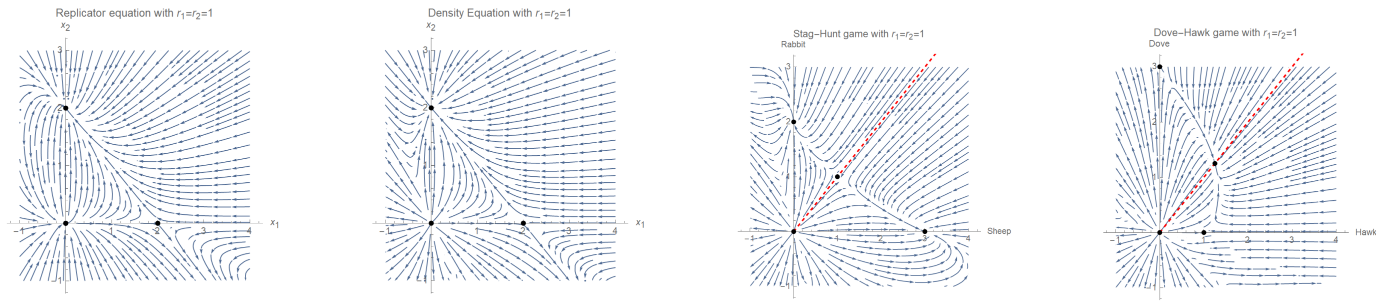
B. Analysis of Internal equilibrium with equal growth rates and its invariance w.r.t growth rates

Solving for fixed points in our 2D density equations, we get:

$$(x_1^*, x_2^*) = (a, 0), (0, c), \left(\frac{(d-b)\Delta}{(a-c+d-b)^2}, \frac{(a-c)\Delta}{(a-c+d-b)^2}\right)$$

Where $\Delta = ad - bc$ is the payoff determinant.

[1]Let $P(S_1, S_2)$ be the payoff of S_1 against S_2. A strategy S* is evolutionarily stable if $P(S*, S*) > P(S, S*)$, or $P(S*, S*) = P(S, S*)$ and $P(S*, S) > P(S, S)\ \forall S \neq S*$



(a) Replicator equation with two monomorphic equilibrium.

(b) Density equation with two monomorphic equilibrium.

(c) Stag-hunt game with a=4,c=3,b=1,d=2

(d) Dove-hawk game with a=1,c=2,b=4,d=3

Fig. 1: Stability of internal equilibrium exhibiting unstable and stable equilibrium as predicted analytically.

We have already analysed the two monomorphic equilibrium. Now, we proceed to analyse the internal equilibrium where both the species coexist. The total population at the internal equilibrium is:

$$x_T = \frac{\Delta}{a-c+d-b}$$

Now, existence of an internal equilibrium is possible iff $a \neq c, d \neq b, sign(a-c) = sign(d-b)$.

If $a = c$ or $d = b$, the internal equilibrium merges with one of the monomorphic equilibrium and if a-c have opposite sign to d-b then one of the species will have negative population ratio which is unphysical. Linear analysis about the internal fixed point gives the characteristic trace and det as:

$$\tau_J = \frac{-r_1(c(2b-d)-ab)}{\Delta}, \Delta_J = \frac{-r_1^2(a-c)(d-b))}{\Delta}$$

If $a > c$ and $d > b$ then, $\Delta > 0, \Delta_J < 0$. So we have a saddle node. If $a < c$ and $d < b$ then, $\Delta < 0, \Delta_J > 0, (c(2b-d)-ab) < 0, \tau_J < 0$. Hence, we have an attracting internal equilibrium. Fig. 1(c),(d) illustrates the dynamics predicted for the same prisoner's Dilemma played by two species with equal growth rates. Since the growth rate is always a positive quantity, it doesn't affect the stability of the internal equilibrium if both species have same equal rates. Hence, this model behaves like the replicator equation for the internal equilibrium as well under equal growth rates.

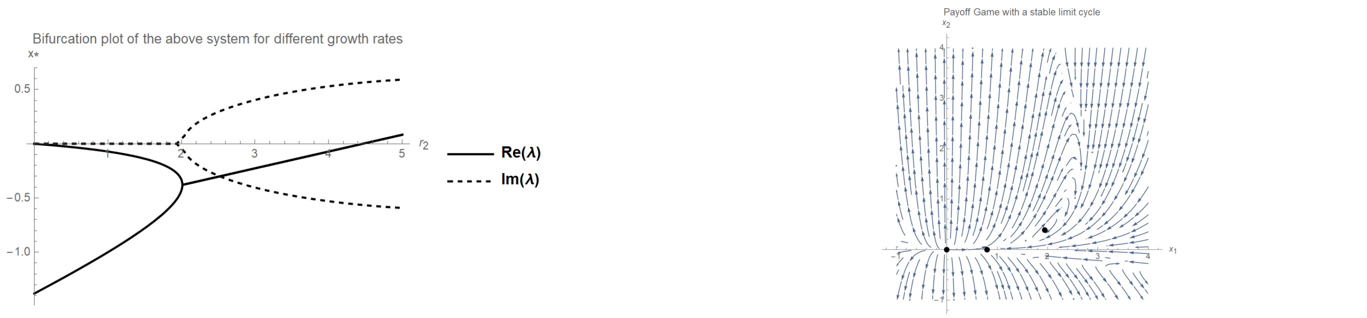
C. Analysis of unequal growth rates and conditions for influence of growth rates

Till now, our density model showed no difference in the dynamics of the species predicted by the replicator equations. But now, we shall show that density equation shows that a fixed point can change its stability by the two species having different growth rates. Replicator only asserts that growth rates can change the time taken to reach an equilibrium but not its stability or location. However, it turns out that in a game where species are too densely packed, the species with more growth rate can significantly affect the coexistence of our two species. Furthermore, unequal growth rates can also lead to limit cycles in our system.

We shall analytically get the conditions for our growth rates to affect the stability of the internal equilibrium. Assuming $r_1 \neq r_2$ we have from linear analysis the characteristic trace and det as:

$$\tau_J = -\frac{(d-b)\alpha_1 r_1 + (a-c)\alpha_2 r_2}{(a-c+d-b)\Delta}, \Delta_J = -\frac{(a-c)(d-b)r_1 r_2}{\Delta}$$

where $\alpha_1 = \Delta + (a-c)(b-a), \alpha_2 = \Delta + (d-b)(c-d)$ are two constants dependent on the payoff that we shall use to analyse the effect of unequal growth rates. We see that Δ_J is not affected by the growth rates since both are positive quantities multiplied to the expression in RHS. So, the effect of growth rates is only implicit in τ_J.



(a) Bifurcation plot of the internal eigenvalues.

(b) Presence of a limit cycle in our system for $r_1 = 1, r_2 = 5$

Fig. 2: Numerical analysis of a game where growth rares affect the stability of internal point

1) Case 1: Both $\alpha_1, \alpha_2 > 0$. In this case, we demand the fact that $sign(a - c) = sign(d - b) = 1$. Reason why their signs can't be -1 is provided in Appendix-B.
2) Case 2: Both $\alpha_1, \alpha_2 < 0$. In this case, we demand the fact that $sign(a-c) = sign(d-b) = -1$. The reasonong follows as in Case: 1 by taking advantage of monotonicity of the p.d w.r.t r_1, r_2.
3) Case 3: α_1, α_2 have opposite signs. This is the only case where τ_J can change signs depending on the value of $(d - b)\alpha_1 r_1 + (a - c)\alpha_2 r_2$. Here, the growth rates explicitly enter into the play to decide the sign of τ_J, and hence the stability of our internal equilibrium.

If our game falls in Case 1 or Case 2, the system will have an internal equilibrium independent of the individual growth rates since $\tau_J < 0$ for both and $sign(\Delta_J)$ is independent of r_i. For case 1, $\Delta_J < 0$ so it will be a saddle node while for case 2, $\Delta_J > 0$ and it will be a stable attractor. But if our payoff is such that the corresponding $\alpha_1 * \alpha_2 < 0$, we have a possibility of getting either a stable or unstable equilibrium depending on the growth rates. Now that we have exactly solved all cases in our 2D density game, we provide examples of growth rates influencing our species dynamics.

D. *Example of a growth rate dependent system*

Consider the payoff with $a = 0.8, b = 10, c = 1, d = 9$. $\alpha_1 = -4.64, \alpha_2 = 5.2$. This system has possibility of changing the stability of its internal equilibrium depending on individual growth rates. We consider $r_1 = 1$ and see the effect of the eigenvalues if we change r_2. Since $a - c, d - b < 0$, we expect it to start with negative eigenvalues implying stable point. Fig. 2(a) numerically plots the bifurcation plot of the two eigenvalues about the internal point and Fig. 2(b) plots a limit cycle as predicted.

We observe that as we change the growth rate r_2, the system changes from a stable attractor to stable cycle at $r_2 \approx 2$, and the cycle changes its stability at $r_2 \approx 4.46$. And on increasing it further, the stable cycle changes to an unstable one, exhibiting Hopf bifurcation. Hence, growth rate clearly affects the internal equilibrium's stability and hence, the dynamics of our evolutionarily competing species.

III. What could the authors have done more?

1) The authors have not considered the fact that the forest have limiting resources explicitly. Although this is implicitly present in the payoffs, more knowledge can be obtained if they separate the factor of competition, and the limiting resources in the carrying capacity used in density equations. In my talk PDF, I have tried to propose a model that considers both these effects by two different parameters, and showed it to successfully predict physical results in case of monomorphic equilibrium. However, the analysis on internal equilibrium could not be done.
2) The authors could have mentioned the practicality of this equation in our ecosystems. Although it predicts interesting dynamics theoretically, it would be more appreciable if these are tested in real life evolutionary dynamics of two species.

IV. Appendix

A. Defining the density equation

The standard replicator for N-competing species is defined as

$$\dot{y_i} = r_i y_i \left(\sum_j a_{ij} y_j - \sum_{i,j} a_{ij} y_i y_j \right) = r_i y_i (f_i - \bar{f}) \tag{2}$$

Where y_i is the frequency or the fraction of ith species in the population, r_i is the growth rate of ith species, f_i is the fitness of the ith species determined by the payoff matrix $A = a_{ij}$, and $\bar{f}$ is the average fitness of the entire population. We also assume the total population remains constant here. Density equation introduces a population dependent carrying capacity, and the removal of the constrain:

$$\sum_i x_i = x_T \neq c_0$$

where x_i is the no.of species i in the population.

Density equation:

$$\dot{x_i} = r_i x_i \left(1 - \frac{x_T}{K_i} \right) \tag{3}$$

where K_i is the carrying capacity of ith species given by:

$$K_i = \sum_j a_{ij} \frac{x_j}{x_T} = \sum_j a_{ij} y_j$$

We shall henceforth consider the case of 2D system with two competing species and play a game with payoff defined by:

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

B. To prove claims in Case 1 and Case 2 for unequal growth rates

Consider the partial derivatives w.r.t each growth rates:

$$\frac{\partial \tau_J(r_1, r_2)}{\partial r_1} = -\frac{(d-b)\alpha_1}{(a-c+d-b)\Delta}$$

$$\frac{\partial \tau_J(r_1, r_2)}{\partial r_2} = -\frac{(a-c)\alpha_2}{(a-c+d-b)\Delta}$$

Adding these partial derivatives gives us:

$$\frac{\partial \tau_J(r_1, r_2)}{\partial r_1} + \frac{\partial \tau_J(r_1, r_2)}{\partial r_2} = -\frac{b(a-c) + c(d-b)}{\Delta}$$

This value is always negative since if $a-c$ and $d-b$ have positive signs, $\Delta = ad - bc > 0$ and the RHS is negative. Similarly, if $a-c$ and $d-b$ have negative signs then $\Delta < 0$ and the RHS remains negative. $a-c$ and $d-b$ cannot have opposite signs since then internal equilibrium wont exist. Now if we consider $a-c$ and $d-b < 0$ for $\alpha_1, \alpha_2 > 0$, then $\frac{\partial \tau_J(r_1, r_2)}{\partial r_1}$, $\frac{\partial \tau_J(r_1, r_2)}{\partial r_2}$ individually are positive and their sum cannot be negative, hence a contradiction.

C. Codes to obtain the results

Code for Replicator Equation solutions for a payoff Game with equal growth rates:

```
a = 2;
b = 1;
c = 4;
d = 2;
sol = Solve[{r1 x1 (a x1 + b x2 -
          1/2 (a x1^2 + d x2^2 + (b + c ) x1 x2)) == 0,
      r2 x2 (c x1 + d x2 - 1/2 (a x1^2 + d x2^2 + (b + c ) x1 x2)) ==
       0}, {x1, x2}] // Simplify // Quiet;
sol = Drop[sol, 1]
StreamPlot[{Subscript[r, 1] Subscript[x,
    1] (a Subscript[x, 1] + b Subscript[x, 2] -
      1/2 (a Subscript[x, 1]^2 +
         d Subscript[x, 2]^2 + (b + c ) Subscript[x, 1] Subscript[x,
          2])), Subscript[r, 2] Subscript[x,
    2] (c Subscript[x, 1] + d Subscript[x, 2] -
      1/2 (a Subscript[x, 1]^2 +
         d Subscript[x, 2]^2 + (b + c ) Subscript[x, 1] Subscript[x,
          2]))} /. {Subscript[r, 1] -> 1,
   Subscript[r, 2] -> 1}, {Subscript[x, 1], -1, 4}, {Subscript[x,
  2], -1, 3},
 PlotLabel ->
  "Replicator equation with \!\(\*SubscriptBox[\(r\), \
\(1\)]\)=\!\(\*SubscriptBox[\(r\), \(2\)]\)=1", Axes -> True,
 Frame -> False,
 AxesLabel -> {"\!\(\*SubscriptBox[\(x\), \(1\)]\)",
   "\!\(\*SubscriptBox[\(x\), \(2\)]\)"},
 Epilog -> {
   {PointSize[0.02], Point[{x1, x2} /. sol]},
   , {PointSize[0.02], Point[{0, 0}]}
   }
 , StreamPoints -> Fine]
```

Code for Density Equation solutions for a payoff Game with equal growth rates:

```
a = 2;
b = 1;
c = 4;
d = 2;
sol = Solve[{(r1 x1)/(a x1 + b x2) (a x1 + b x2 - (x1 + x2)^2) ==
     0, (r2 x2)/(c x1 + d x2) (c x1 + d x2 - (x1 + x2)^2) == 0}, {x1,
    x2}] // Simplify
StreamPlot[{(
    Subscript[r, 1] Subscript[x,
     1])/(a Subscript[x, 1] + b Subscript[x, 2]) (a Subscript[x, 1] +
      b Subscript[x, 2] - (Subscript[x, 1] + Subscript[x, 2])^2), (
    Subscript[r, 2] Subscript[x, 2])/(
    c Subscript[x, 1] +
     d Subscript[x, 2]) (c Subscript[x, 1] +
      d Subscript[x,
       2] - (Subscript[x, 1] + Subscript[x, 2])^2)} /. {Subscript[r,
    1] -> 1, Subscript[r, 2] -> 1}, {Subscript[x, 1], -1,
  4}, {Subscript[x, 2], -1, 3},
 PlotLabel ->
  "Density Equation with \!\(\*SubscriptBox[\(r\), \
```

```
\(1\)]\)=\!\(\*SubscriptBox[\(r\), \(2\)]\)=1", Axes -> True,
 Frame -> False,
 AxesLabel -> {"\!\(\*SubscriptBox[\(x\), \(1\)]\)",
   "\!\(\*SubscriptBox[\(x\), \(2\)]\)"},
 Epilog -> {
   {PointSize[0.02], Point[{x1, x2} /. sol]},
   , {PointSize[0.02], Point[{0, 0}]}
   }
 , StreamPoints -> Fine]
```

Jacobian for deriving the eigenvalues of monomorphic equilibrium:

```
Clear[a, b, c, d]
f = Subscript[r, 1] Subscript[x,
   1] (1 - (Subscript[x, 1] + Subscript[x, 2])^2/(
     a Subscript[x, 1] + b Subscript[x, 2]));
g = Subscript[r, 2] Subscript[x,
   2] (1 - (Subscript[x, 1] + Subscript[x, 2])^2/(
     c Subscript[x, 1] + d Subscript[x, 2]));
sol = Solve[{(r1 x1)/(a x1 + b x2) (a x1 + b x2 - (x1 + x2)^2) ==
      0, (r2 x2)/(c x1 + d x2) (c x1 + d x2 - (x1 + x2)^2) == 0}, {x1,
      x2}] // Simplify // Quiet
J = {{D[f, Subscript[x, 1]],
    D[f, Subscript[x, 2]]}, {D[g, Subscript[x, 1]],
    D[g, Subscript[x, 2]]}};
J = J /. {Subscript[x, 1] -> 0, Subscript[x, 2] -> d} // Simplify;
Eigenvalues[J]

Code for obtaining the effect of internal equilibrium on changing payoff parameter c:

\begin{minted}{python}
a = 2;
b = 1;
d = 2;
Manipulate[
 sol = Solve[{(r1 x1)/(a x1 + b x2) (a x1 + b x2 - (x1 + x2)^2) ==
       0, (r2 x2)/(c x1 + d x2) (c x1 + d x2 - (x1 + x2)^2) ==
       0}, {x1, x2}] // Simplify // Quiet;
 StreamPlot[{(
     Subscript[r, 1] Subscript[x,
      1])/(a Subscript[x, 1] + b Subscript[x, 2]) (a Subscript[x, 1] +
        b Subscript[x, 2] - (Subscript[x, 1] + Subscript[x, 2])^2), (
     Subscript[r, 2] Subscript[x, 2])/(
     c Subscript[x, 1] +
      d Subscript[x, 2]) (c Subscript[x, 1] +
       d Subscript[x,
        2] - (Subscript[x, 1] + Subscript[x, 2])^2)} /. {Subscript[r,
      1] -> 1, Subscript[r, 2] -> 1}, {Subscript[x, 1], -1,
    4}, {Subscript[x, 2], -1, 3},
  PlotLabel -> "Density Equation for: a=2, b=1, d=2", Axes -> True,
  Frame -> False,
  AxesLabel -> {"\!\(\*SubscriptBox[\(x\), \(1\)]\)",
    "\!\(\*SubscriptBox[\(x\), \(2\)]\)"},
  Epilog -> {
    {PointSize[0.02], Point[{x1, x2} /. sol]},
    , {PointSize[0.02], Point[{0, 0}]}
    }
  , StreamPoints -> Fine],
```

```
 {{c, 4}, 0, 5}]
```

Code for obtaining the phase portrait of Dove-Hawk game with equal growth rates:

```
a = 1;
b = 4;
c = 2;
d = 3;
sol = Solve[{(r1 x1)/(a x1 + b x2) (a x1 + b x2 - (x1 + x2)^2) ==
     0, (r2 x2)/(c x1 + d x2) (c x1 + d x2 - (x1 + x2)^2) == 0}, {x1,
    x2}] // Simplify
StreamPlot[{(
    Subscript[r, 1] Subscript[x,
     1])/(a Subscript[x, 1] + b Subscript[x, 2]) (a Subscript[x, 1] +
      b Subscript[x, 2] - (Subscript[x, 1] + Subscript[x, 2])^2), (
    Subscript[r, 2] Subscript[x, 2])/(
    c Subscript[x, 1] +
     d Subscript[x, 2]) (c Subscript[x, 1] +
      d Subscript[x,
       2] - (Subscript[x, 1] + Subscript[x, 2])^2)} /. {Subscript[r,
    1] -> 1, Subscript[r, 2] -> 1}, {Subscript[x, 1], -1,
  4}, {Subscript[x, 2], -1, 3},
 PlotLabel ->
  "Hawk-Dove Game with \!\(\*SubscriptBox[\(r\), \
\(1\)]\)=\!\(\*SubscriptBox[\(r\), \(2\)]\)=1", Axes -> True,
 Frame -> False, AxesLabel -> {"Hawk", "Dove"},
 Epilog -> {
   {Red, Dashed, Thickness[0.006],
    Line[{{0, 0}, {4, 4 (a - c)/(d - b)}}]},
   {PointSize[0.02], Point[{x1, x2} /. sol]},
   , {PointSize[0.02], Point[{0, 0}]}
   }
 , StreamPoints -> Fine]
```

Jacobian about internal point:

```
Clear[a, b, c, d]
f = Subscript[r, 1] Subscript[x,
   1] (1 - (Subscript[x, 1] + Subscript[x, 2])^2/(
     a Subscript[x, 1] + b Subscript[x, 2]));
g = Subscript[r, 2] Subscript[x,
   2] (1 - (Subscript[x, 1] + Subscript[x, 2])^2/(
     c Subscript[x, 1] + d Subscript[x, 2]));
sol = Solve[{(r1 x1)/(a x1 + b x2) (a x1 + b x2 - (x1 + x2)^2) ==
       0, (r2 x2)/(c x1 + d x2) (c x1 + d x2 - (x1 + x2)^2) ==
       0}, {x1, x2}] // Simplify // Quiet;

J = {{D[f, Subscript[x, 1]],
    D[f, Subscript[x, 2]]}, {D[g, Subscript[x, 1]],
    D[g, Subscript[x, 2]]}};
J // MatrixForm
```

Linear analysis for equal growth rates:

```
Clear[a, b, c, d]
Det[J /. {Subscript[x, 1] -> ((b - d) (b c - a d))/(a - b - c + d)^2,
     Subscript[x, 2] -> ((a - c) (-b c + a d))/(a - b - c + d)^2,
     Subscript[r, 2] -> Subscript[r, 1]}] // Simplify // MatrixForm
Tr[J /. {Subscript[x, 1] -> ((b - d) (b c - a d))/(a - b - c + d)^2,
```

```
     Subscript[x, 2] -> ((a - c) (-b c + a d))/(a - b - c + d)^2,
     Subscript[r, 2] -> Subscript[r, 1]}] // Simplify // MatrixForm
```

Linear analysis about internal equilibrium for unequal growth rates:

```
Det[J /. {Subscript[x, 1] -> ((b - d) (b c - a d))/(a - b - c + d)^2,
     Subscript[x, 2] -> ((a - c) (-b c + a d))/(a - b - c + d)^2}] //
  Simplify // MatrixForm
Tr[J /. {Subscript[x, 1] -> ((b - d) (b c - a d))/(a - b - c + d)^2,
     Subscript[x, 2] -> ((a - c) (-b c + a d))/(a - b - c + d)^2}] //
  Simplify // MatrixForm
```

Derivative of Tr(J(Subscript[r, 1], Subscript[r, 2])):

```
{D[-(((d-b)Subscript[\[Alpha], 1] Subscript[r, 1]+(a-c) Subscript[\[Alpha], 2] Subscript[r, 2])/((a-b-c+
```

Code for the bifurcation plot of the example system:

```
a = 0.8;
b = 10;
c = 1;
d = 9;
Subscript[r, 1] = 1;
eqn = x^2 -
    Tr[J /. {Subscript[x,
         1] -> ((b - d) (b c - a d))/(a - b - c + d)^2,
        Subscript[x,
         2] -> ((a - c) (-b c + a d))/(a - b - c + d)^2}] x +
    Det[J /. {Subscript[x,
        1] -> ((b - d) (b c - a d))/(a - b - c + d)^2,
       Subscript[x,
        2] -> ((a - c) (-b c + a d))/(a - b - c + d)^2}] == 0;
sol = NSolve[eqn, x];
Plot[{Re[x /. sol], Im[x /. sol]}, {Subscript[r, 2], 0, 5},
 PlotLabel ->
  "Bifurcation plot of the above system for different growth rates",
 PlotStyle -> {{Black, Thick}, {Dashed, Black, Thick}},
 PlotLegends -> {"Re(\[Lambda])", "Im(\[Lambda])"},
 AxesLabel -> {"\!\(\*SubscriptBox[\(r\), \(2\)]\)", "x*"}]
```

Code for obtaining an attracting cycle:

```
Clear[x, y]
a = 0.8;
b = 10;
c = 1;
d = 9;
sol = Solve[{(r1 x1)/(a x1 + b x2) (a x1 + b x2 - (x1 + x2)^2) ==
     0, (r2 x2)/(c x1 + d x2) (c x1 + d x2 - (x1 + x2)^2) == 0}, {x1,
    x2}] // Simplify
StreamPlot[{(
    Subscript[r, 1] Subscript[x,
     1])/(a Subscript[x, 1] + b Subscript[x, 2]) (a Subscript[x, 1] +
      b Subscript[x, 2] - (Subscript[x, 1] + Subscript[x, 2])^2), (
    Subscript[r, 2] Subscript[x, 2])/(
    c Subscript[x, 1] +
     d Subscript[x, 2]) (c Subscript[x, 1] +
      d Subscript[x,
       2] - (Subscript[x, 1] + Subscript[x, 2])^2)} /. {Subscript[r,
```

```
   1] -> 1, Subscript[r, 2] -> 5}, {Subscript[x, 1], -1,
 4}, {Subscript[x, 2], -1, 4},
PlotLabel -> "Payoff Game with a stable limit cycle", Axes -> True,
Frame -> False,
AxesLabel -> {"\!\(\*SubscriptBox[\(x\), \(1\)]\)",
  "\!\(\*SubscriptBox[\(x\), \(2\)]\)"},
Epilog -> {
  {PointSize[0.02], Point[{x1, x2} /. sol]},
  , {PointSize[0.02], Point[{0, 0}]}
  }
, StreamPoints -> Fine]
```