MSc Computational Methods in Ecology and Evolution

Ecological Modelling: Introduction to dynamical systems

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Question 1. The Harvest equation

A modification of the logistic equation gives the Harvest equation, for a population x, for example of fish, where at a constant rate c fish are removed or harvested:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = vx\left(1 - \frac{x}{K}\right) - c.$$

A bifurcation is a change in the nature or number of fixed points, as a parameter of the ODE is varied. The Harvest equation exhibits what is known as a saddle-node bifurcation as the parameter c is varied, where two fixed points merge to one and then disappear as c is decreased.

a) Put this equation in non-dimensional form
$$\frac{dz}{d\tau} = z(1 - z) - \eta$$
using $\tau = vt$ and $z = x/K$, where you should find $\eta = \frac{c}{vK}$. Interpret what this constant η means.

b) Sketch the phase portrait of this ODE for i) $\eta < \frac{1}{4}$, ii) $\eta = \frac{1}{4}$, and iii) $\eta > \frac{1}{4}$, by plotting the RHS of above equation as function of z, and determining the position and stability of each fixed point (if there are any).

c) For each of i, ii, and iii, use these phase portraits to plot solution curves, an initial condition z_0, where for:
   - i) I) $z_1 < z_0 < \frac{1}{2}$, II) $\frac{1}{2} < z_0 < z_2$, III) $z_0 > z_2$, IV) $z_0 < z_1$, V) $z_0 = z_2$, VI) $z_0 = z_1$, where z_1 is the fixed point closest to the origin and z_2 is the other fixed point;
   - ii) I) $z_0 > \frac{1}{2}$, II) $z_0 < \frac{1}{2}$, and III) $z_0 = \frac{1}{2}$
   - iii) I) $z_0 > \frac{1}{2}$, and II) $z_0 < \frac{1}{2}$,

   taking care to use the information on how $\frac{\mathrm{d}z}{\mathrm{d}t}$ changes over time as solution progresses to obtain the qualitatively correct curvature ($\frac{\mathrm{d}^2z}{\mathrm{d}t^2}$).

d) For each of i, ii and iii, determine whether a long-term population of fish is viable and if so for which initial population sizes? Express your answer in terms of the original non-scaled variables and comment on the robustness of these answers to perturbations or stochasticity in the system.

e) If $c = 1000$ fish per day, $v =$ [redacted] fish per day and $\cancel{x_{max}}\,K = 10000$ fish, is there long-term viability of the populations and if so above which critical initial frequency?

f) Finally, apart from some conclusions being non-robust to perturbations, what other unrealistic feature does this model have and what can be done to rectify it?

v = 0.1/day

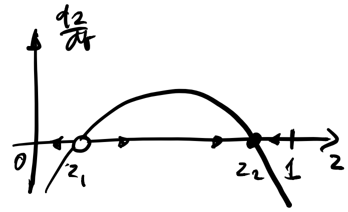
a) $v\dfrac{d(Kz)}{d\tau} = vK\,z(1-z) - c$

$$\Rightarrow \frac{dz}{d\tau} = z(1-z) - \frac{c}{vK} = z(1-z) - \eta \; ; \; \eta = \frac{c}{vK}$$

- η is the ratio of rate fish are removed to the rate of growth of maximum population

b) Want to plot $z(1-z)-\eta$ vs z : it is 1st helpful to note that for $\eta=0$ the maximum of $z(1-z)$ is at $z=1/2$ & the maximum value is $\frac{1}{2}(1-\frac{1}{2})=\frac{1}{4}$

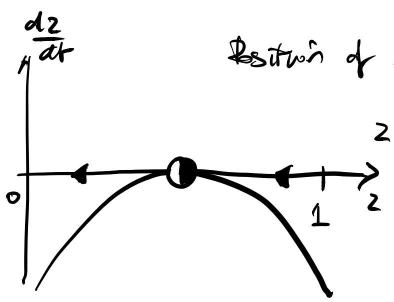
i) $\eta < \frac{1}{4}$



Position of fixed points:

$$\left.\begin{aligned} & z(1-z)-\eta = 0 \\ & z^2 - z + \eta = 0 \\ & z = \frac{1 \pm \sqrt{1-4\eta}}{2} \end{aligned}\right\} \quad \begin{aligned} z_1 &= \frac{1-\sqrt{1-4\eta}}{2} \quad \text{UNSTABLE} \\ z_2 &= \frac{1+\sqrt{1-4\eta}}{2} \quad \text{STABLE} \end{aligned}$$

ii) $\eta = 1/4$

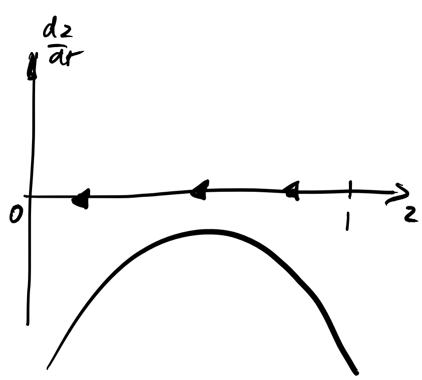


Position of fixed point for $\eta = 1/4$:

$$z(1-z)-\eta = 0 \;\rightarrow\; z = \frac{1 \pm \sqrt{1-4\eta}}{2} = \frac{1}{2}$$

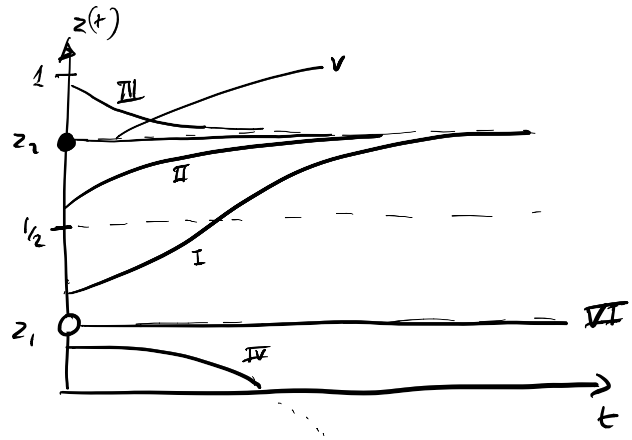
HALF-STABLE

iii) $\eta > 1/4$.



NO FIXED POINTS

c) i)



I) $z_1 < z_0 < \frac{1}{2}$

* According to phase-portrait $z(t)$ must increase monotonically to fixed point z_2

$\Rightarrow$ On this trajectory $\frac{dz}{dt}$ increases until $z = \frac{1}{2}$ $\Rightarrow$ solution has an initially convex (upwards) curvature

when $z(t) > \frac{1}{2}$ $\frac{dz}{dt}$ is decreasing & so the curve should have a concave (downwards) curvature

II) $\frac{1}{2} < z_0 < z_2$

* Again solution $z(t)$ increases monotonically to z_2, & on this trajectory $\frac{dz}{dt}$ is decreasing $\Rightarrow$ the solution has a concave (downwards) curvature.

III) $z_0 > z_2$

$z(t)$ decreases monotonically to z_2, where $\frac{dz}{dt}$ is increasing $\Rightarrow$ $\frac{d^2z}{dt^2} > 0$

$\Rightarrow$ solution is convex (upwards) [Alternatively, $\frac{dz}{dt}$ is becoming less & less -ve]

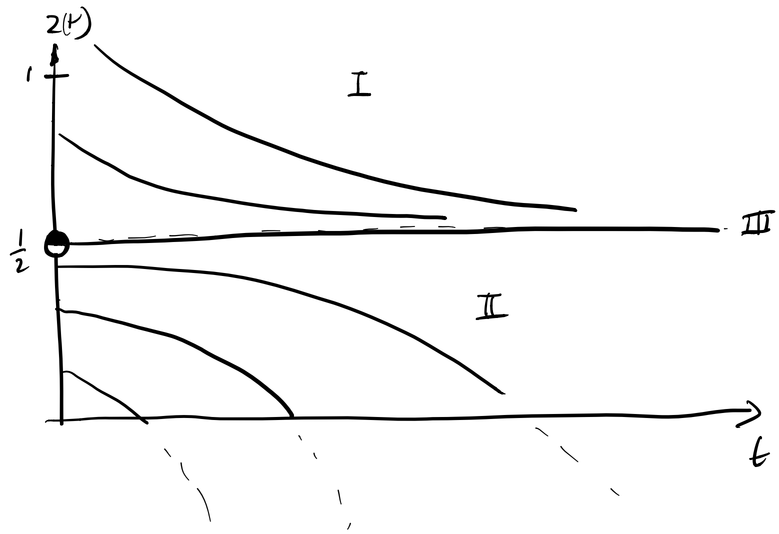
IV) $z_0 < z_1$

$z(t)$ decreases monotonically & $\frac{dz}{dt}$ is decreasing $\Rightarrow$ $\frac{d^2z}{dt^2} < 0$

$\Rightarrow$ solution is concave (downwards) [OR, $\frac{dz}{dt}$ is becoming more & more -ve]

V) & VI) $\frac{dz}{dt} = 0$ $\Rightarrow$ solutions have zero curvature & are horizontal straight lines.

ii)



I) $z_0 > \frac{1}{2}$

$z(t)$ decreases monotonically, where $\frac{dz}{dt} > 0$ for $z(t) > \frac{1}{2}$ & $\Rightarrow \frac{d^2z}{dt^2} > 0$

$\Rightarrow$ for $z(t) > \frac{1}{2}$ solution is convex (upwards) [$\frac{dz}{dt}$ is becoming less & less negative]

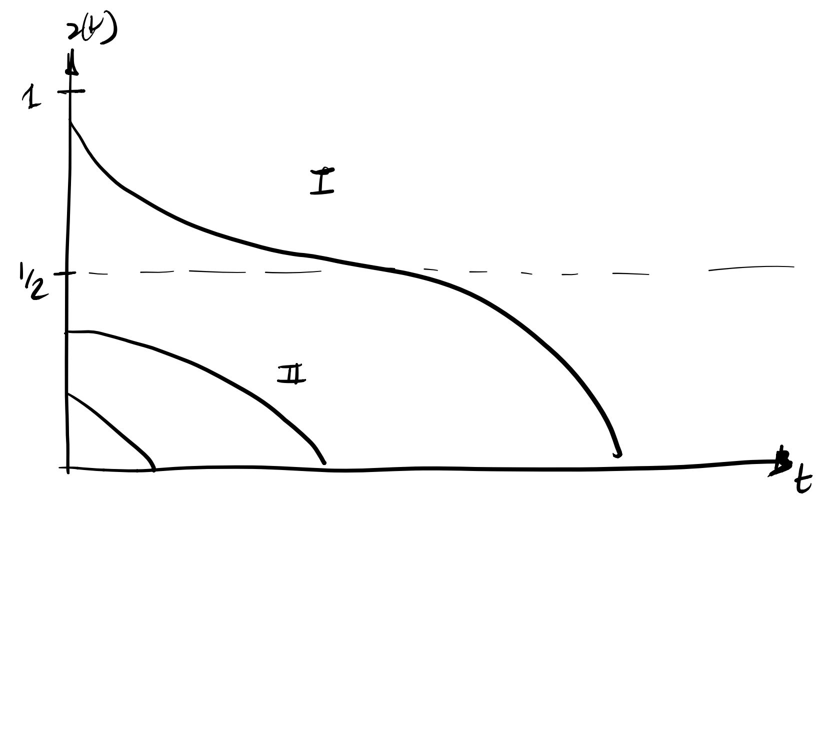
$\rightarrow$ $z(t) \rightarrow \frac{1}{2}$ asymptotically as $t \rightarrow \infty$

II) $z_0 < \frac{1}{2}$

$z(t)$ decreases monotonically & $\frac{dz}{dt} < 0$ $\Rightarrow$ $\frac{d^2z}{dt^2} < 0$ $\Rightarrow$ concave (downwards).

III) $z_0 = \frac{1}{2}$ $\frac{dz}{dt} = 0$

iii)



I) $z_0 > \frac{1}{2}$

$z(t)$ decreases monotonically, where $\frac{dz}{dt} > 0$ for $z(t) > \frac{1}{2}$ & $\Rightarrow \frac{d^2z}{dt^2} > 0$

$\Rightarrow$ for $z(t) > \frac{1}{2}$ solution is convex (upwards) [$\frac{dz}{dt}$ is becoming less & less negative]

for $z(t) > \frac{1}{2}$ $\frac{dz}{dt} < 0 \Rightarrow \frac{d^2z}{dt^2} < 0$ $\Rightarrow$ solution is concave (downwards)

[$\frac{dz}{dt}$ is becoming more and more negative].

II) $z_0 < \frac{1}{2}$ $\quad \frac{dz}{dt} < 0 \Rightarrow \frac{d^2z}{dt^2} < 0$ $\Rightarrow$ solution is concave (downwards)

[$\frac{dz}{dt}$ is becoming more and more negative].

d) i) Population only viable for an initial condition $z_0 > z_1$

$$z_1 = \frac{1 - \sqrt{1-4m}}{2}$$

$$\Rightarrow \frac{n_0}{n_{max}} > \frac{1 - \sqrt{1 - 4c/\sigma K}}{2}$$

$$\Rightarrow n_0 > \frac{K - \sqrt{K^2 - 4\frac{cK}{\sigma}}}{2}$$

ii) Population only viable for an initial condition $z_0 > \frac{1}{2}$

$$\Rightarrow \frac{n_0}{K} > \frac{1}{2} \quad \Rightarrow n_0 > \frac{K}{2}$$

- However, this result is not robust to stochasticity or perturbations as the fixed point $n = \frac{K}{2}$ is unstable

iii) There are no initial conditions for which there is a long term sustainable population.

e) $c = 1000 \quad r = 0.1 \quad K = 10000$

$$\eta = \frac{c}{rK} = \frac{1000}{1000} = 1 > \frac{1}{4}$$

$\Rightarrow$ there is no long-term viable population

f) A constant catch per day may be unrealistic.
A catch per day in proportion to the population size may be more realistic.

Question 2 Lotka-Volterra dynamics

If $x(t)$ is the population of prey and $y(t)$ is the population of the predator the coupled ODEs describing their dynamics are

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \dot{x} = f(x,y) = \alpha x - \gamma xy$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = \dot{y} = g(x,y) = \kappa\gamma xy - \beta y$$

a) Draw the nullclines (lines that define $\dot{x} = 0$ and $\dot{y} = 0$) and find the fixed points of these ODEs (excluding the *trivial* one which is $x^* = y^* = 0$), which are defined by the values of x^* & y^*, where the two nullclines cross.

b) The $\dot{x} = 0$ nullcline indicates where on the x-y plane where the phase curves are is purely vertical (↕) and the $\dot{y} = 0$ nullcline indicates where on the x-y plane where the phase curve is purely horizontal (↔). Determine the actual direction of phase curve on nullclines, by examining for the $\dot{x} = 0$ nullcline whether $\dot{y} < 0, or\ \dot{y} > 0$, and for the $\dot{y} = 0$ nullcline whether $\dot{x} < 0, or\ \dot{x} > 0$, by examining the original equations. At this stage what type of solutions do the nullclines indicate? (Refer to the classification of types of dynamics: node, spiral, centre, etc..)

c) We want to write down linearised versions of the above ODEs near the fixed point x^*, y^*. Evaluate the two-variable Taylor expansion to 1st order for $f(x,y)$ and $g(x,y)$

$$f(x,y) = f(x^*,y^*) + \left(\frac{\partial f}{\partial x}\right)_{x=x^*,y=y^*}(x-x^*) + \left(\frac{\partial f}{\partial y}\right)_{y=y^*,x=x^*}(y-y^*) = -\frac{\beta}{\kappa}(y-y^*)$$
$$g(x,y) = g(x^*,y^*) + \left(\frac{\partial g}{\partial x}\right)_{x=x^*,y=y^*}(x-x^*) + \left(\frac{\partial g}{\partial y}\right)_{y=y^*,x=x^*}(y-y^*) = \kappa\alpha(x-x^*)$$

Why are the terms $f(x^*,y^*) = g(x^*,y^*) = 0$?

d) Let $\delta x = x - x^*$ & $\delta y = y - y^*$, show that $\dot{\delta x} = \dot{x}$ and $\dot{\delta y} = \dot{y}$ and make the substitution above to give the matrix equation

$$\begin{pmatrix}\dot{\delta x}\\ \dot{\delta y}\end{pmatrix} = \begin{pmatrix}0 & -\beta/\kappa\\ \kappa\alpha & 0\end{pmatrix}\begin{pmatrix}\delta x\\ \delta y\end{pmatrix}$$

e) Let the matrix above be $\boldsymbol{J}$ (in mathematics, this matrix is known as the Jacobian and in ecology the community matrix). Show that its eigenvalues are

$$\lambda = i\omega = \pm i\sqrt{\beta\alpha}$$

What do the imaginary eigenvalues tell you about the dynamics?

f) It is possible to calculate a solution to these dynamics near the fixed point, by calculating the complex eigenvectors, but we expect the solutions will be elliptical (as the off-diagonal elements are not equal), we can use the results of the previous question to write the solution as motion on an ellipse. Show that the solution to the linearised matrix equation, for initial condition $\delta x(0) = \delta x_0$ and $\delta y(0) = \delta y_0$, is

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \boldsymbol{RU}(\omega t)\boldsymbol{R}^{-1}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$
$$= \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix}\begin{pmatrix} \cos\omega t & -\sin\omega t \\ \sin\omega t & \cos\omega t \end{pmatrix}\begin{pmatrix} 1/R_1 & 0 \\ 0 & 1/R_2 \end{pmatrix}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

where $R_1 = \sqrt{\frac{\beta}{\kappa}}R$ & $R_2 = \sqrt{\kappa\alpha}R.$

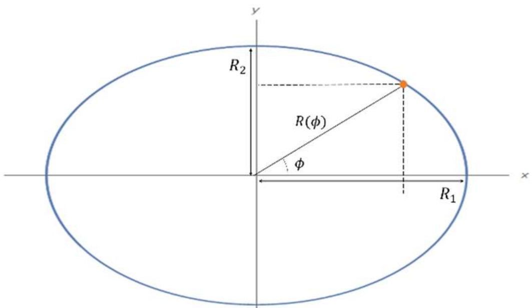
g) Given that the equation for an ellipse is

$$\left(\frac{\delta x_0}{R_1}\right)^2 + \left(\frac{\delta y_0}{R_2}\right)^2 = 1$$

Show that $R = \sqrt{\frac{\delta x_0^2}{\beta/\kappa} + \frac{\delta y_0^2}{\kappa\alpha}}$

h) The last relation $R = \sqrt{\frac{\delta x_0^2}{\beta/\kappa} + \frac{\delta y_0^2}{\kappa\alpha}}$ indicates that for different initial conditions the overall size of the orbits changes. *Mathematically*, why is this unrealistic for large R? Why could this be also unrealistic for empirical biological/ecological reasons?

*Question 3 Parametric equation for an ellipse



An ellipse can be obtained from a unit circle by stretching along the x-direction by R_1 and y-direction by R_2 ; if $R_1 > R_2$, then $R_1$is the major axis of the ellipse and R_2 is the minor axis.

Points on an ellipse are defined by

$$\left(\frac{x}{R_1}\right)^2 + \left(\frac{y}{R_2}\right)^2 = 1 \tag{1}$$

In Q2 h) if we set $x_0 = R, y_0 = 0$ then we have a simple parameterisation of the motion along a circle

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} R\cos\omega t \\ R\sin\omega t \end{pmatrix}$$

a) Argue that the equivalent parameterisation for an ellipse is
$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} R_1\cos\omega t \\ R_2\sin\omega t \end{pmatrix}$$
b) i) Why is the angle $\phi = \tan^{-1}\left(\frac{y}{x}\right) \neq \theta = \omega t$? ii) What is θ in terms of x, y, R_1, R_2?
c) To obtain an equivalent expression as in Q2 h), why can we not simply use a rotation matrix $\boldsymbol{U}(\omega t)$ multiplying an initial position vector $\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$?

d) What effect does the diagonal matrix $\boldsymbol{R} = \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix}$ have on the basis vectors $\underline{e}_1$ & $\underline{e}_2$?

e) What is $\boldsymbol{R}^{-1}$and what effect does it have on the basis vectors $\underline{e}_1$ & $\underline{e}_2$?

f) If the initial position vector $\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$ lies on an ellipse with major and minor axis R_1 and R_2 (which we can ensure by making sure it obeys Eqn.1), calculate $\underline{u} = \boldsymbol{R}^{-1}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$. Show that it now lies on a unit circle by calculating the magnitude of the vector.

g) Take the result $\underline{u}$ and calculate $\underline{r} = \boldsymbol{U}(\omega t)\underline{u}$. Where does the vector $\underline{r}$ lie on the plane?

h) Now calculate the result of $\boldsymbol{R}\underline{r}$. Where does this lie on the plane – verify that the point lies on the ellipse given by Eqn.1

i) Putting the results of f),g) & h) together show that

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \boldsymbol{R}\boldsymbol{U}(\omega t)\boldsymbol{R}^{-1}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$
$$= \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix}\begin{pmatrix} \cos\omega t & -\sin\omega t \\ \sin\omega t & \cos\omega t \end{pmatrix}\begin{pmatrix} 1/R_1 & 0 \\ 0 & 1/R_2 \end{pmatrix}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

j) Show using Eqn. 1 that to ensure x_0, y_0 lie on ellipse

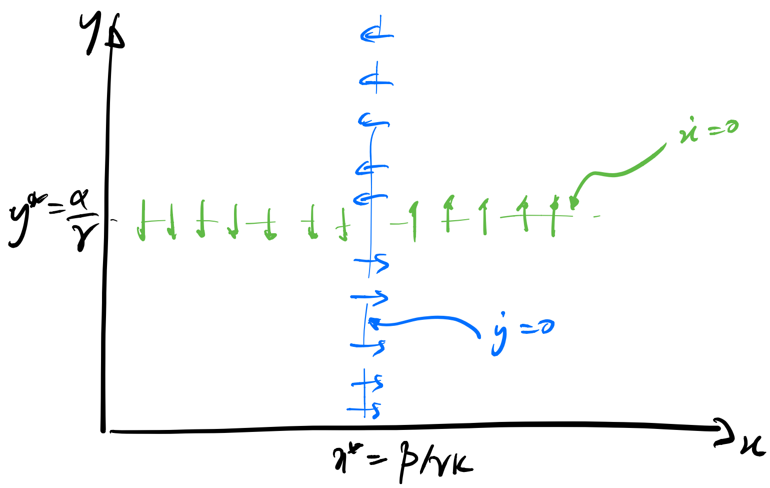
$$y_0 = \pm R_2\sqrt{1 - \left(\frac{x_0}{R_1}\right)^2}$$

k) Expand out as a vector the LHS of i) and using your favourite software do a parametric plot of $y(t)$ vs $x(t)$, for various values of R_1, R_2, ω, x_0

2a) Need to find fixed points of both eqns.

$\Rightarrow \dot{x} = \frac{dx}{dt} = 0 \Rightarrow \alpha \cancel{x} = \gamma \cancel{x} y \Rightarrow y^* = \frac{\alpha}{\gamma}$ ($\dot{x} = 0$ nullcline)

$\dot{y} = \frac{dy}{dt} = 0 \Rightarrow \beta \cancel{y} = k\gamma x \cancel{y} \Rightarrow x^* = \frac{\beta}{\gamma k}$ ($\dot{y} = 0$ nullcline)



On $\dot{x} = 0$ nullcline

b) * On $\dot{x} = 0$ nullcline $y^* = \frac{\alpha}{\gamma}$. $\Rightarrow \dot{y} = k\gamma x y^* - \beta y^*$

$$= \frac{k\alpha \cancel{\gamma} x}{\cancel{\gamma}} - \frac{\beta\alpha}{\gamma}$$

$$= k\alpha x - \frac{\beta\alpha}{\gamma}$$

$$= \alpha k (x - x^*)$$

$\Rightarrow \dot{y} > 0$ if $x > x^*$

$\dot{y} < 0$ if $x < x^*$

* On $\dot{y} = 0$ nullcline $x^* = \beta/k\gamma \Rightarrow \dot{x} = \alpha x^* - \gamma x^* y$

$$= \alpha \frac{\beta}{\gamma k} - \cancel{\gamma} \frac{\beta}{\cancel{\gamma} k} y$$

$$= -\frac{\beta}{k}(y - y^*)$$

$\Rightarrow \dot{x} > 0$ if $y < y^*$

$\dot{x} < 0$ if $y > y^*$

→ Using this information you can plot the direction of the arrows in diagram above (phase plane) as shown.

→ The direction field on the nullclines indicate oscillatory solutions.

c) Evaluate partial derivatives.

$$\left.\frac{\partial f}{\partial x}\right|_{x^*,y^*} = \left.\frac{\partial}{\partial x}(\alpha x - \gamma x y)\right|_{x^*,y^*} = \alpha - \gamma y\Big|_{y^*} = 0$$

$$\left.\frac{\partial f}{\partial y}\right|_{x^*,y^*} = \left.\frac{\partial}{\partial y}(\alpha x - \gamma x y)\right|_{x^*,y^*} = -\gamma x\Big|_{x^*} = -\cancel{\gamma}\cdot\frac{\beta}{\cancel{\gamma}k} = -\frac{\beta}{k}$$

$$\left.\frac{\partial g}{\partial x}\right|_{x^*,y^*} = \left.\frac{\partial}{\partial x}(k\gamma x y - \beta y)\right|_{x^*,y^*} = k\gamma y\Big|_{y^*} = k\cancel{\gamma}\frac{\alpha}{\cancel{\gamma}} = k\alpha$$

$$\left.\frac{\partial g}{\partial y}\right|_{x^*,y^*} = \left.\frac{\partial}{\partial y}(k\gamma x y - \beta y)\right|_{x^*,y^*} = k\gamma x - \beta\Big|_{x^*} = 0.$$

$$\Rightarrow f(x,y) = f(x^*,y^*) + \left.\frac{\partial f}{\partial x}\right|_{x^*,y^*}(x-x^*) + \left.\frac{\partial f}{\partial y}\right|_{x^*,y^*}(y-y^*)$$

$$= -\frac{\beta}{k}(y-y^*)$$

$$g(x,y) = g(x^*,y^*) + \left.\frac{\partial g}{\partial x}\right|_{x^*,y^*}(x-x^*) + \left.\frac{\partial g}{\partial y}\right|_{x^*,y^*}(y-y^*)$$

$$= k\alpha(x-x^*)$$

d) $\delta x = x - x^*$ & $\delta y = y - y^*$

$$\Rightarrow \delta\dot{x} = \dot{x} - \underbrace{\cancel{\dot{x}^*}}_{=0} = \dot{x} \quad \Rightarrow \delta\dot{x} = -\frac{\beta}{k}(y-y^*) = -\frac{\beta}{k}\delta y$$

$$\delta\dot{y} = \dot{y} - \underbrace{\cancel{\dot{y}^*}}_{=0} = \dot{y} \quad \Rightarrow \delta\dot{y} = k\alpha(x-x^*) = k\alpha\,\delta x.$$

→ We can put this in the following matrix eqn.

$$\begin{pmatrix} \dot{\delta x} \\ \dot{\delta y} \end{pmatrix} = \begin{pmatrix} 0 & -\beta/K \\ K\alpha & 0 \end{pmatrix} \begin{pmatrix} \delta x \\ \delta y \end{pmatrix}$$

e)

$$\begin{pmatrix} 0 & -\omega_1^2 \\ \omega_2^2 & 0 \end{pmatrix}$$

$$\Rightarrow \underline{\underline{J}} = \begin{pmatrix} 0 & -\beta/K \\ K\alpha & 0 \end{pmatrix}$$

Eigenvalues : $|\underline{\underline{J}} - \lambda \underline{\underline{I}}| = 0$.

$$\Rightarrow \lambda^2 + \omega_1^2\omega_2^2 = 0,$$
$$\Rightarrow \lambda = \pm\sqrt{-\omega_1^2\omega_2^2}$$
$$= \pm i\,\omega_1\omega_2 \qquad = \pm i\sqrt{\beta\alpha}$$

$$\Rightarrow \begin{vmatrix} -\lambda & -\beta/K \\ K\alpha & -\lambda \end{vmatrix} = 0$$

$$\lambda^2 + \alpha\beta = 0 \Rightarrow \lambda = \pm\sqrt{-\alpha\beta} = \pm i\sqrt{\beta\alpha}$$

Let $\omega = \sqrt{\beta\alpha}$

→ Imaginary eigenvalues show that the solutions in phase-plane are rotational & → oscillatory in δx & δy.

f) $$\begin{pmatrix}\delta x\\ \delta y\end{pmatrix} = \begin{pmatrix}R_1 & 0\\ 0 & R_2\end{pmatrix}\begin{pmatrix}\cos\omega t & -\sin\omega t\\ \sin\omega t & \cos\omega t\end{pmatrix}\begin{pmatrix}1/R_1 & 0\\ 0 & 1/R_2\end{pmatrix}\begin{pmatrix}\delta x_0\\ \delta y_0\end{pmatrix}$$

$\underline{LHS}$

$$\frac{d}{dt}\begin{pmatrix}x\\ y\end{pmatrix} = \begin{pmatrix}R_1 & 0\\ 0 & R_2\end{pmatrix}\begin{pmatrix}\frac{d}{dt}\cos\omega t & \frac{d}{dt}(-\sin\omega t)\\ \frac{d}{dt}(\sin\omega t) & \frac{d}{dt}(\cos\omega t)\end{pmatrix}\begin{pmatrix}1/R_1 & 0\\ 0 & 1/R_2\end{pmatrix}\begin{pmatrix}\delta x_0\\ \delta y_0\end{pmatrix}$$

$$= \begin{pmatrix}R_1 & 0\\ 0 & R_2\end{pmatrix}\begin{pmatrix}-\omega\sin\omega t & -\omega\cos\omega t\\ \omega\cos\omega t & -\omega\sin\omega t\end{pmatrix}\begin{pmatrix}1/R_1 & 0\\ 0 & 1/R_2\end{pmatrix}\begin{pmatrix}\delta x_0\\ \delta y_0\end{pmatrix}$$

$$= -\omega\begin{pmatrix}R_1 & 0\\ 0 & R_2\end{pmatrix}\begin{pmatrix}\sin\omega t & \cos\omega t\\ -\cos\omega t & \sin\omega t\end{pmatrix}\begin{pmatrix}1/R_1 & 0\\ 0 & 1/R_2\end{pmatrix}\begin{pmatrix}\delta x_0\\ \delta y_0\end{pmatrix}$$

$$= -\omega\begin{pmatrix}R_1 & 0\\ 0 & R_2\end{pmatrix}\begin{pmatrix}\sin\omega t & \cos\omega t\\ -\cos\omega t & \sin\omega t\end{pmatrix}\begin{pmatrix}\frac{\delta x_0}{R_1}\\ \delta y_0/R_2\end{pmatrix}$$

$$= -\omega\begin{pmatrix}R_1 & 0\\ 0 & R_2\end{pmatrix}\begin{pmatrix}\frac{\delta x_0}{R_1}\sin\omega t + \frac{\delta y_0}{R_2}\cos\omega t\\ -\frac{\delta x_0}{R_1}\cos\omega t + \frac{\delta y_0}{R_2}\sin\omega t\end{pmatrix}$$

$$= -\omega\begin{pmatrix}\delta x_0\sin\omega t + \frac{R_1}{R_2}\delta y_0\cos\omega t\\ -\frac{R_2}{R_1}\delta x_0\cos\omega t + \delta y_0\sin\omega t\end{pmatrix}$$

$\omega = \sqrt{\beta\alpha}$

$$= \begin{pmatrix}-\sqrt{\beta\alpha}\,\delta x_0\sin\omega t - \sqrt{\beta\alpha}\,\frac{R_1}{R_2}\delta x_0\cos\omega t\\ +\sqrt{\beta\alpha}\,\frac{R_2}{R_1}\delta x_0\cos\omega t + \sqrt{\beta\alpha}\,\delta y_0\sin\omega t\end{pmatrix}$$

$$= \begin{pmatrix}-\sqrt{\beta\alpha}\,\delta x_0\sin\omega t - \frac{\beta}{k}\delta x_0\cos\omega t\\ k\alpha\,\delta x_0\cos\omega t + \sqrt{\beta\alpha}\,\delta y_0\sin\omega t\end{pmatrix}$$

$R_1 = \sqrt{\frac{\beta}{k}}\,R$

$R_2 = \sqrt{k\alpha}\,R.$

$\Rightarrow \frac{R_1}{R_2} = \frac{\sqrt{\beta/k}}{\sqrt{k\alpha}}$

$= \frac{1}{k}\sqrt{\frac{\beta}{\alpha}}$

$\Rightarrow \frac{R_2}{R_1} = k\sqrt{\frac{\alpha}{\beta}}$

RHS

$$\underline{\underline{J}} = \begin{pmatrix} 0 & -\beta/k \\ k\alpha & 0 \end{pmatrix}$$

$$\Rightarrow \underline{\underline{J}} \begin{pmatrix} \delta x \\ \delta y \end{pmatrix} = \begin{pmatrix} 0 & -\beta/k \\ k\alpha & 0 \end{pmatrix} \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix} \begin{pmatrix} \cos\omega t & -\sin\omega t \\ \sin\omega t & \cos\omega t \end{pmatrix} \begin{pmatrix} 1/R_1 & 0 \\ 0 & 1/R_2 \end{pmatrix} \begin{pmatrix} \delta x_0 \\ \delta y_0 \end{pmatrix}$$

$$= \begin{pmatrix} 0 & -\beta/k \\ k\alpha & 0 \end{pmatrix} \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix} \begin{pmatrix} \cos\omega t & -\sin\omega t \\ \sin\omega t & \cos\omega t \end{pmatrix} \begin{pmatrix} \frac{\delta x_0}{R_1} \\ \frac{\delta y_0}{R_2} \end{pmatrix}$$

$$= \begin{pmatrix} 0 & -\beta/k \\ k\alpha & 0 \end{pmatrix} \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix} \begin{pmatrix} \frac{\delta x_0}{R_1} \cos\omega t - \frac{\delta y_0}{R_2} \sin\omega t \\ \frac{\delta x_0}{R_1} \sin\omega t + \frac{\delta y_0}{R_2} \cos\omega t \end{pmatrix}$$

$$= \begin{pmatrix} 0 & -\beta/k \\ k\alpha & 0 \end{pmatrix} \begin{pmatrix} \delta x_0 \cos\omega t - \frac{R_1}{R_2} \delta y_0 \sin\omega t \\ \frac{R_2}{R_1} \delta x_0 \sin\omega t + \delta y_0 \cos\omega t \end{pmatrix}$$

$$= \begin{pmatrix} -\frac{\beta}{k}\frac{R_2}{R_1} \delta x_0 \sin\omega t - \frac{\beta}{k} \delta y_0 \cos\omega t \\ k\alpha\, \delta x_0 \cos\omega t - k\alpha \frac{R_1}{R_2} \delta y_0 \sin\omega t \end{pmatrix}$$

$$\frac{R_1}{R_2} = \frac{1}{k}\sqrt{\frac{\beta}{\alpha}}$$

$$\frac{R_2}{R_1} = k\sqrt{\frac{\alpha}{\beta}}$$

$$= \begin{pmatrix} -\sqrt{\beta\alpha}\, \delta x_0 \sin\omega t - \beta/k\, \delta y_0 \cos\omega t \\ k\alpha\, \delta x_0 \cos\omega t - \sqrt{\beta\alpha}\, \delta y_0 \sin\omega t \end{pmatrix}$$

$\Rightarrow$ LHS = RHS //

g)

$\Rightarrow$ where axis of ellipse $R_1 = R\sqrt{\frac{\beta}{K}}$ & $R_2 = R\sqrt{K\alpha}$

$$\Rightarrow \quad \frac{\delta x_0^2}{R_1^2} + \frac{\delta y_0^2}{R_2^2} = 1$$

$$\Rightarrow \quad \frac{\delta x_0^2}{R^2 \frac{\beta}{K}} + \frac{\delta y_0^2}{R^2 K\alpha} = 1$$

$$\Rightarrow R^2 = \frac{\delta x_0^2}{\beta/K} + \frac{\delta y_0^2}{K\alpha}$$

$$\Rightarrow R = \sqrt{\frac{\delta x_0^2}{\beta/K} + \frac{\delta y_0^2}{K\alpha}}$$

g) Orbits whose size "R" depends on the initial conditions are called "neutrally stable".
Empirically, predator-prey systems are thought to have an intrinsic size to their orbits, called a limit cycle, where different initial condition give rise to the same sized orbit.
For this reason, the Lotka-Volterra model is thought to be unrealistic. However, if demographic fluctuations are accounted for, more realistic limit-cycle type behaviour can arise, as shown in (McKane & Newman, PRL, 2005, 94)

3a) Compared to a unit circle distances along x-axis are magnified ($R_1 > 1$) or contracted ($R_1 < 1$) by factor R_1 & along y-axis magnified ($R_2 > 1$) or contracted ($R_2 < 1$) by factor R_2

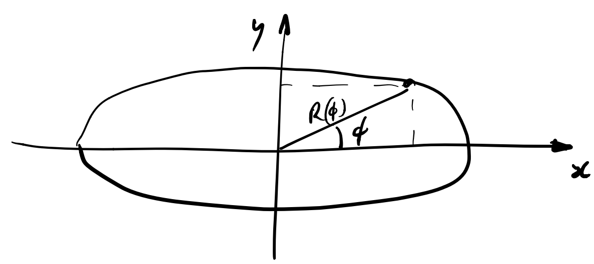
$\Rightarrow$ the images of the basis vectors are $\underline{r}_1 = R_1 \underline{e}_1$
& $\underline{r}_2 = R_2 \underline{e}_2$

$\Rightarrow$ We can multiply the vector representing motion along a unit circle $\begin{pmatrix} \cos\omega t \\ \sin\omega t \end{pmatrix}$ by $(\underline{r}_1, \underline{r}_2) = \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix}$

$$\Rightarrow \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix} \begin{pmatrix} \cos\omega t \\ \sin\omega t \end{pmatrix}$$

$$= \begin{pmatrix} R_1 \cos\omega t \\ R_2 \sin\omega t \end{pmatrix}$$

b) i)



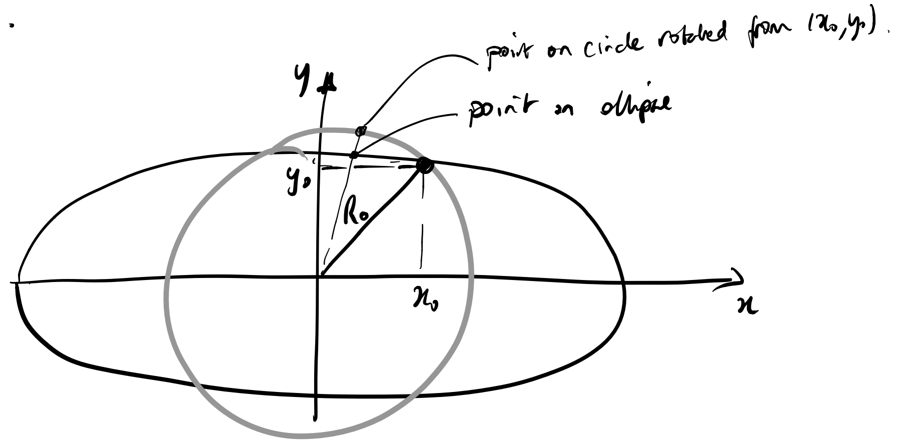
$\tan(\phi) = \dfrac{R_2 \sin\omega t}{R_1 \cos\omega t}$ is the angle the point on the ellipse makes w.r.t. to the x-axis, while

$\tan(\theta) = \dfrac{\cos\omega t}{\sin\omega t}$ is the phase angle of motion on a circle which increases linearly with time $\theta = \omega t$.

→ ϕ does not change linearly with time

ii) $\theta = \omega t = \tan^{-1}\left(\frac{\sin\omega t}{\cos\omega t}\right) = \tan^{-1}\left(\frac{y/R_2}{x/R_1}\right)$

c) If we start with any point (x_0, y_0) on the ellipse, such that $R_0^2 = x_0^2 + y_0^2$, any rotation matrix by definition, then must act to rotate this point without dilation, but the length of the vector on the ellipse must change as it goes around the ellipse.



d) See answer to a)

e) $\underline{\underline{R}}^{-1} = \begin{pmatrix} 1/R_1 & 0 \\ 0 & 1/R_2 \end{pmatrix}$ it multiplies distances along x-axis by $1/R_1$
" " " y-axis by $1/R_2$

f) $\underline{u} = \underline{\underline{R}}^{-1}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$

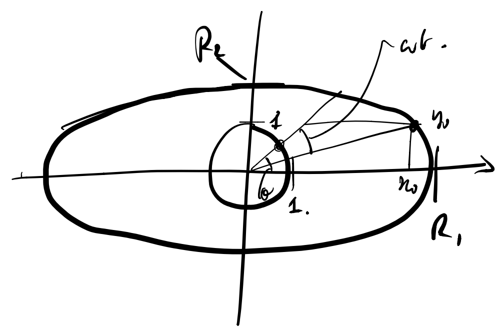
$$= \begin{pmatrix} 1/R_1 & 0 \\ 0 & 1/R_2 \end{pmatrix}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} = \begin{pmatrix} x_0/R_1 \\ y_0/R_2 \end{pmatrix}$$

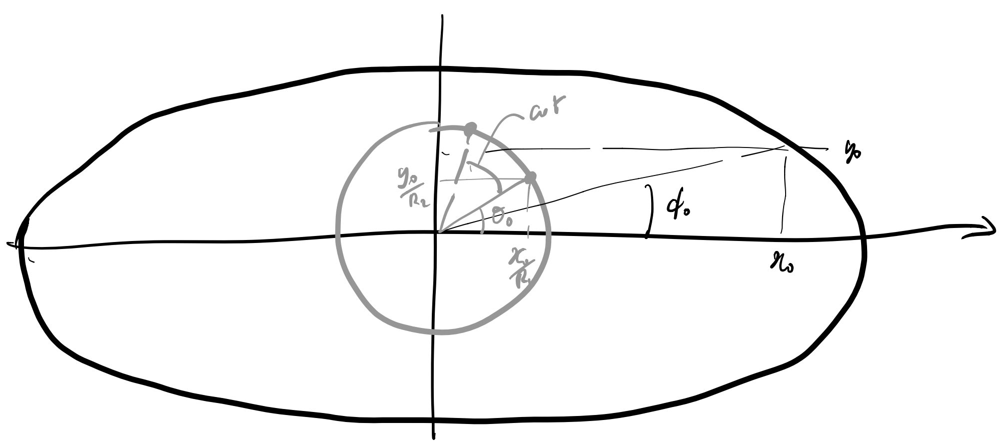
$$u_1^2 + u_2^2 = \left(\frac{x_0}{R_1}\right)^2 + \left(\frac{y_0}{R_2}\right)^2 = 1 \quad \text{i.e magnitude of } |\underline{u}| = 1.$$

g) $\underline{r} = \underline{\underline{U}}(\omega t)\,\underline{u}$

$$= \begin{pmatrix} \cos\omega t & -\sin\omega t \\ \sin\omega t & \cos\omega t \end{pmatrix} \begin{pmatrix} x_0/R_1 \\ y_0/R_2 \end{pmatrix}$$

$$= \begin{pmatrix} \dfrac{x_0 \cos\omega t}{R_1} - \dfrac{y_0 \sin\omega t}{R_2} \\[2ex] \dfrac{x_0 \sin\omega t}{R_1} + \dfrac{y_0 \cos\omega t}{R_2} \end{pmatrix}$$





$\Rightarrow$ it is a vector on unit circle at an angle

$$\theta = \underbrace{\tan^{-1}\left(\frac{y_0/R_2}{x_0/R_1}\right)}_{\text{initial angle } \theta_0 \ (\neq \phi_0)} + \omega t$$

h) $\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \underline{\underline{R}}\,\underline{r} = \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix} \begin{pmatrix} \frac{x_0 \cos\omega t}{R_1} - \frac{y_0 \sin\omega t}{R_2} \\ \frac{x_0 \sin\omega t}{R_1} + \frac{y_0 \cos\omega t}{R_2} \end{pmatrix}$

$$= \begin{pmatrix} R_1\left(\frac{x_0}{R_1} \cos\omega t - \frac{y_0}{R_2} \sin\omega t \right) \\ R_2\left(\frac{x_0}{R_1} \sin\omega t + \frac{y_0}{R_2} \cos\omega t \right) \end{pmatrix}$$

& Want to show this vector lies on ellipse :

$$\Rightarrow \left(\frac{x}{R_1}\right)^2 + \left(\frac{y}{R_2}\right)^2 = 1 .$$

$$LHS = \left(\frac{\cancel{R_1}}{\cancel{R_1}} \left(\frac{x_0}{R_1} \cos\omega t - \frac{y_0}{R_2} \sin\omega t \right) \right)^2 + \left(\frac{\cancel{R_2}}{\cancel{R_2}} \left(\frac{x_0}{R_1} \sin\omega t + \frac{y_0}{R_2} \cos\omega t \right) \right)^2$$

$$= \left(\frac{x_0}{R_1}\right)^2 \cos^2\omega t + \left(\frac{y_0}{R_2}\right)^2 \sin\omega t - \cancel{\frac{2x_0 y_0}{R_1 R_2} \sin\omega t \cos\omega t}$$

$$+ \left(\frac{x_0}{R_1}\right)^2 \sin^2\omega t + \left(\frac{y_0}{R_2}\right)^2 \cos^2\omega t + \cancel{\frac{2x_0 y_0}{R_1 R_2} \sin\omega t \cos\omega t}.$$

$$= \left[\left(\frac{x_0}{R_1}\right)^2 + \left(\frac{y_0}{R_2}\right)^2 \right] \left(\sin^2\omega t + \cos^2\omega t \right)$$

$$= \left(\frac{x_0}{R_1}\right)^2 + \left(\frac{y_0}{R_2}\right)^2 = 1 \;//$$

i) $$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \underline{\underline{R}}\,\underline{r}$$
$$= \underline{\underline{R}}\,\underline{\underline{U}}(\omega t)\,\underline{u}$$
$$= \underline{\underline{R}}\,\underline{\underline{U}}(\omega t)\,\underline{\underline{R}}^{-1}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$
$$= \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix}\begin{pmatrix} \cos\omega t & -\sin\omega t \\ \sin\omega t & \cos\omega t \end{pmatrix}\begin{pmatrix} 1/R_1 & 0 \\ 0 & 1/R_2 \end{pmatrix}\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

j) $$\left(\frac{x_0}{R_1}\right)^2 + \left(\frac{y_0}{R_2}\right)^2 = 1.$$

$$\Rightarrow \left(\frac{y_0}{R_2}\right)^2 = 1 - \left(\frac{x_0}{R_1}\right)^2$$

$$\Rightarrow \frac{y_0}{R_2} = \pm\sqrt{1 - \left(\frac{x_0}{R_1}\right)^2}$$

$$\Rightarrow y_0 = \pm R_2\sqrt{1 - \left(\frac{x_0}{R_1}\right)^2} \quad //$$