MA 331

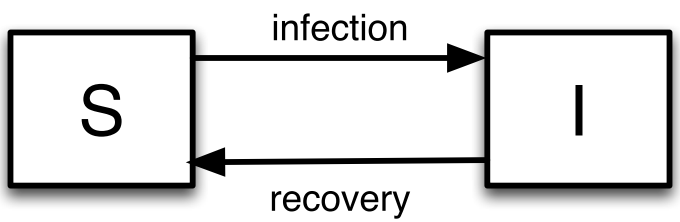
Differential Equations for the Life Sciences

Fall 2018

Lecture 8

SIS Model for a directly transmitted infection

Susceptible/infectious/susceptible model for an infectious disease



Population of N individuals: each is either susceptible (S) or infected and infectious (I)

$N = S + I$ hence: $S = N - I$

Rate at which new infections arise is proportional to both the number of susceptibles and the number of infectives, constant of proportionality β/N

Infectives recover at per-capita rate γ, but have no immunity after recovery

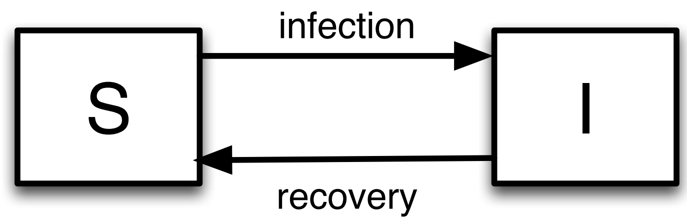
$$\frac{dS}{dt} = -\frac{\beta SI}{N} + \gamma I$$

$$\frac{dI}{dt} = \frac{\beta SI}{N} - \gamma I$$

Because $N = S + I$, we only need one of these two equations… use $S = N - I$ to rewrite the I equation as:

$$\frac{dI}{dt} = \frac{\beta (N - I) I}{N} - \gamma I$$

SIS Model for a directly transmitted infection



$$\frac{dI}{dt} = \frac{\beta(N-I)I}{N} - \gamma I$$

Simplify: $$\frac{dI}{dt} = \beta\left(1 - \frac{I}{N}\right)I - \gamma I$$

Rewrite in terms of $y = I / N$, the fraction of the population that is infectious

$I = N\,y$ $$\frac{dI}{dt} = \frac{d}{dt}\left(Ny\right) = N\frac{dy}{dt}$$

$$N\frac{dy}{dt} = \beta\left(1-y\right)Ny - \gamma Ny$$

$$\frac{dy}{dt} = \beta\left(1-y\right)y - \gamma y$$

Terminology: we call rate constants (e.g. β and γ) **parameters** of the model

Equilibria of the SIS Model

$$\frac{dy}{dt} = \beta(1-y)y - \gamma y$$

Set $dy/dt = 0$ and solve for y

$$0 = \beta(1-y)y - \gamma y$$

$$0 = y(\beta(1-y) - \gamma)$$

Either $\boxed{y = 0}$ (**infection free equilibrium**)

or $0 = \beta(1-y) - \gamma$

$$\gamma = \beta(1-y)$$

$$\gamma/\beta = 1 - y$$

$$y = 1 - \gamma/\beta$$

Define $R_0 = \beta/\gamma$, the **basic reproductive number**

$$\boxed{y = 1 - 1/R_0}$$

This equilibrium is biologically feasible if $R_0 > 1$
(otherwise, this value of y is negative)

the **endemic equilibrium**

Notice: $R_0 > 1$ if $\beta > \gamma$; $R_0 < 1$ if $\beta < \gamma$

Stability of the Equilibria of the SIS Model $\frac{dy}{dt} = \beta(1-y)y - \gamma y$

We have $y = 0$ and $y = 1 - 1/R_0$, and $g(y) = \beta(1-y)y - \gamma y = \beta y - \beta y^2 - \gamma y$

$$g'(y) = \beta - 2\beta y - \gamma$$

$\boxed{y = 0}$ (infection free equilibrium)

$$g'(0) = \beta - 2\beta \cdot 0 - \gamma \quad = \beta - \gamma$$

$g'(0) < 0$ if $\beta < \gamma$; $g'(0) > 0$ if $\beta > \gamma$

Stable if $\beta < \gamma$; Unstable if $\beta > \gamma$

Recall: $R_0 > 1$ if $\beta > \gamma$; $R_0 < 1$ if $\beta < \gamma$

Infection free equilibrium is stable if $R_0 < 1$; Unstable if $R_0 > 1$

$\boxed{y^* = 1 - 1/R_0}$

$$\begin{aligned} g'(1-1/R_0) &= \beta - 2\beta\left(1 - 1/R_0\right) - \gamma \\ &= \beta - 2\beta\left(1 - \gamma/\beta\right) - \gamma \\ &= -\beta + \gamma \\ &= -\left(\beta - \gamma\right) \end{aligned}$$

$g'(y^*) > 0$ if $\beta < \gamma$; $g'(y^*) < 0$ if $\beta > \gamma$

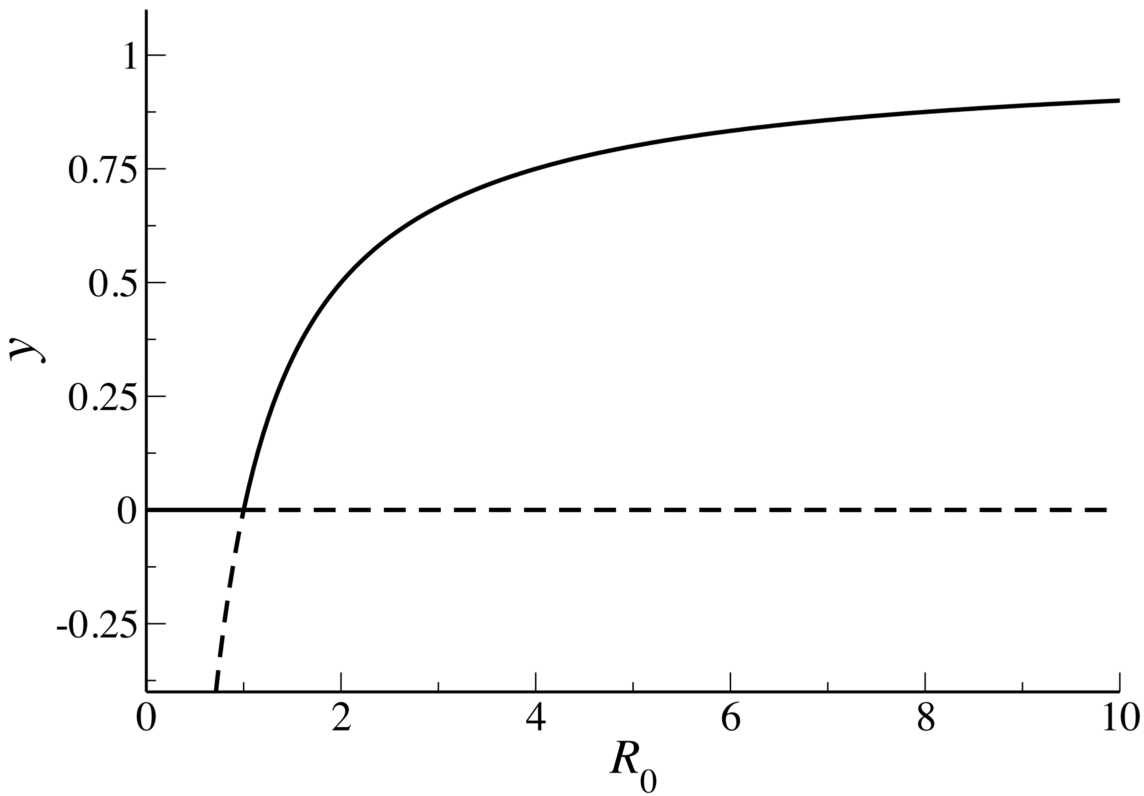
Unstable if $\beta < \gamma$; Stable if $\beta > \gamma$

Endemic equilibrium is unstable (and infeasible) if $R_0 < 1$; Stable (and feasible) if $R_0 > 1$

Bifurcation Diagram: Summarizing Equilibria of SIS Model

Location and stability of the equilibria of the SIS model depend on the parameter R_0

Summarize this on a **bifurcation diagram** that shows equilbria, and their stability, as functions of the parameter



solid lines denote **stable** equilibria

dashed lines denote **unstable** equilibria

Alternative: Graphical Analysis of SIS Model

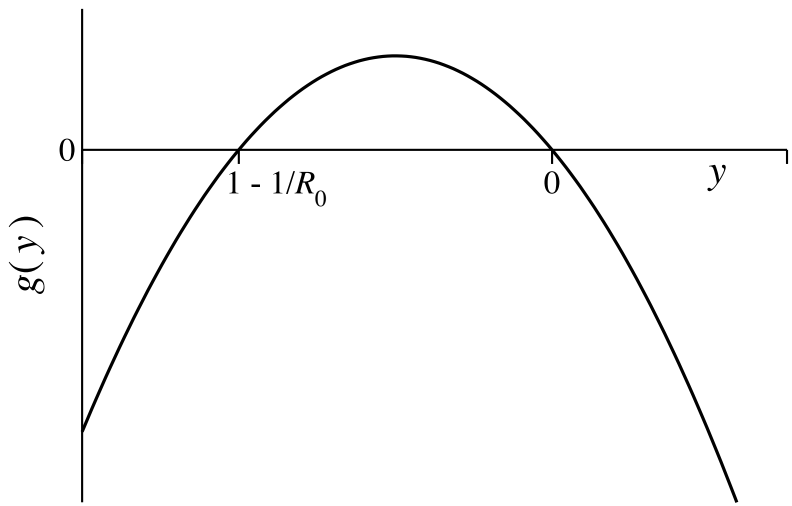
$$\frac{dy}{dt} = \beta(1-y)y - \gamma y$$

Sketch function on right side of differential equation

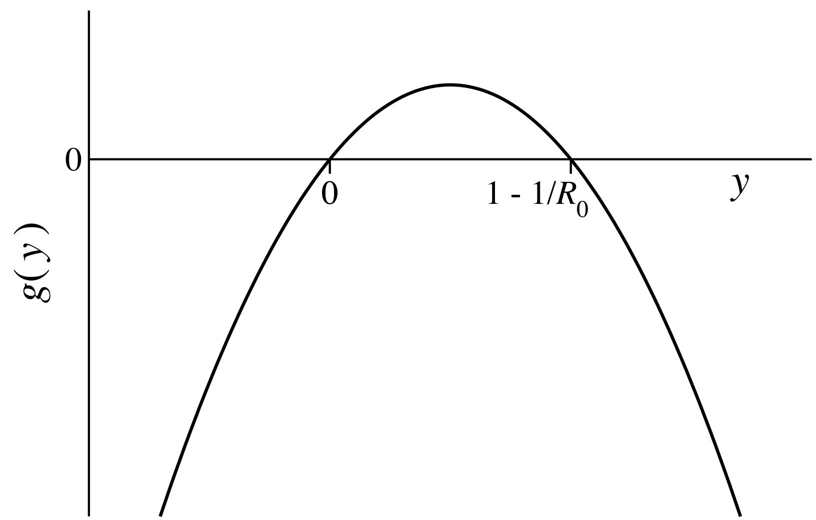
$$g(y) = \beta(1-y)y - \gamma y$$

Downwards parabola, with zeros at $y = 0$ and $y = 1 - 1/R_0$

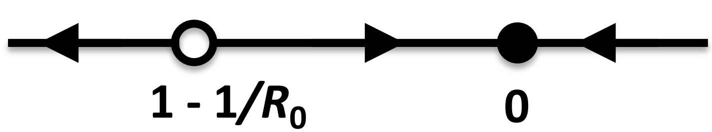
$R_0 < 1$ picture:

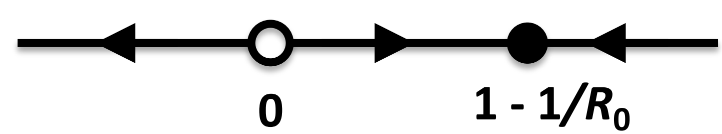


$R_0 > 1$ picture:



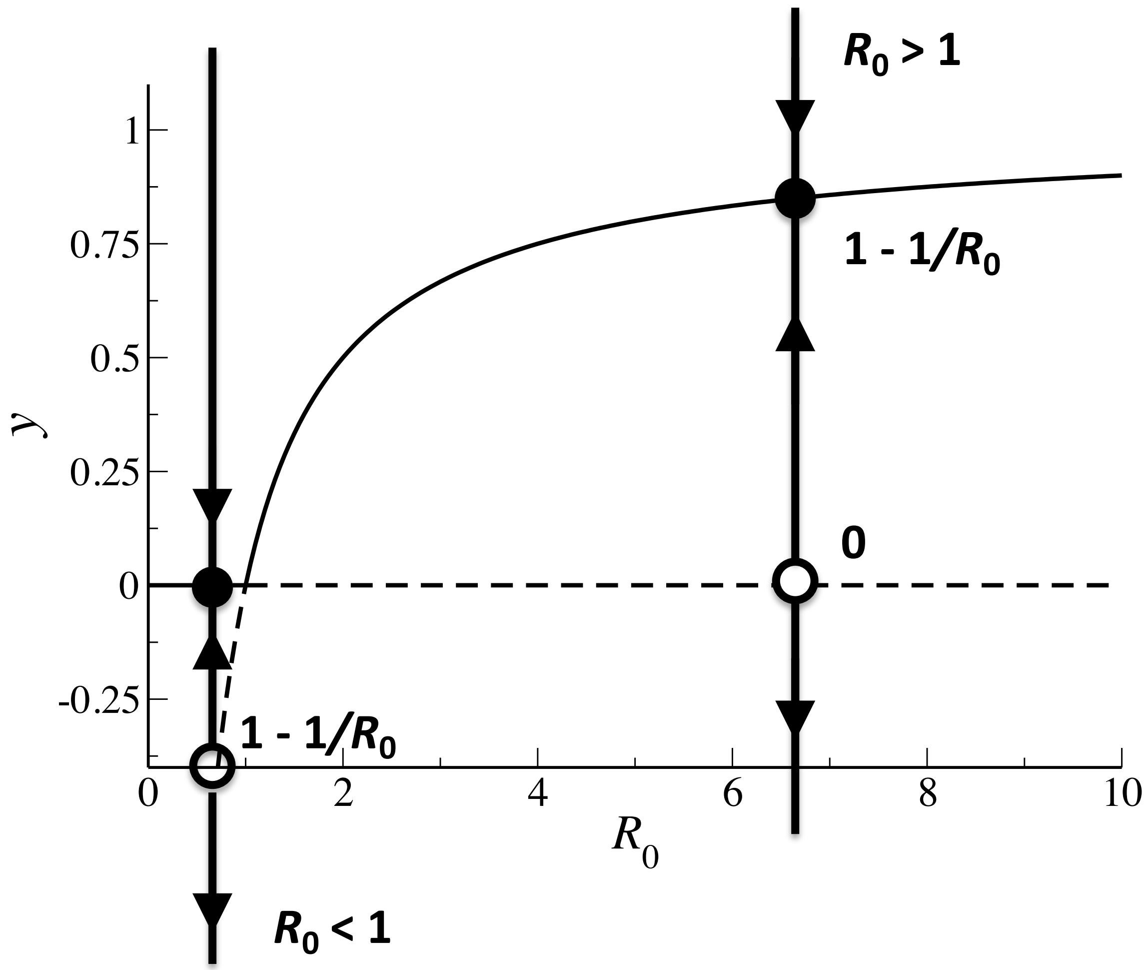
Phase diagrams:



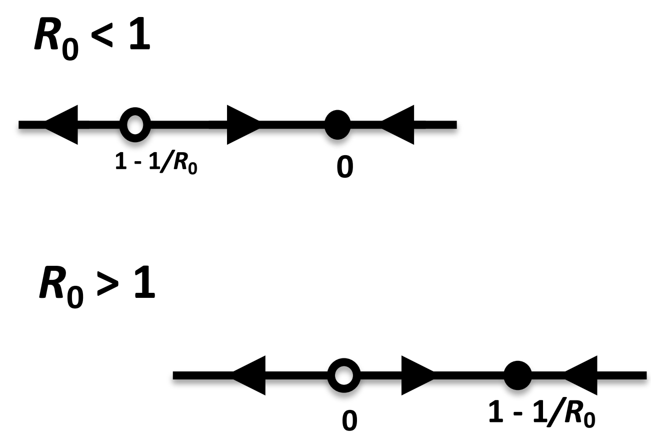


Relationship between Bifurcation Diagram and Phase Diagrams

Can build up the bifurcation diagram by rotating and "stacking up" phase lines for different values of the parameter (here, R_0)

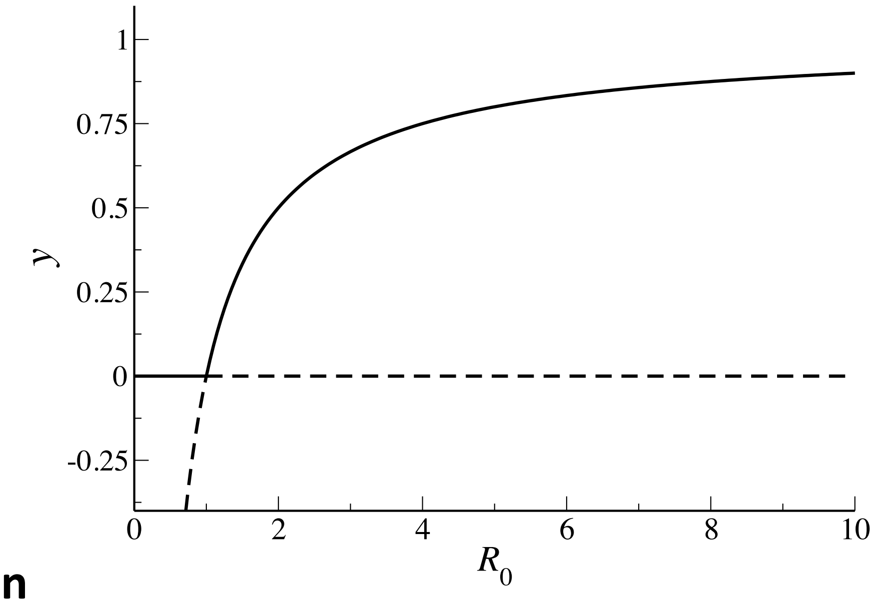


Phase diagrams:



Transcritical (Exchange of Stability) Bifurcation

Bifurcation diagram shows that the **qualitative behavior** of the system **changes** when R_0 passes through 1



A qualitative change in behavior is called a bifurcation

In this case, two equilibria collide and exchange stability: a **transcritical bifurcation**

Bifurcation: "split in two"

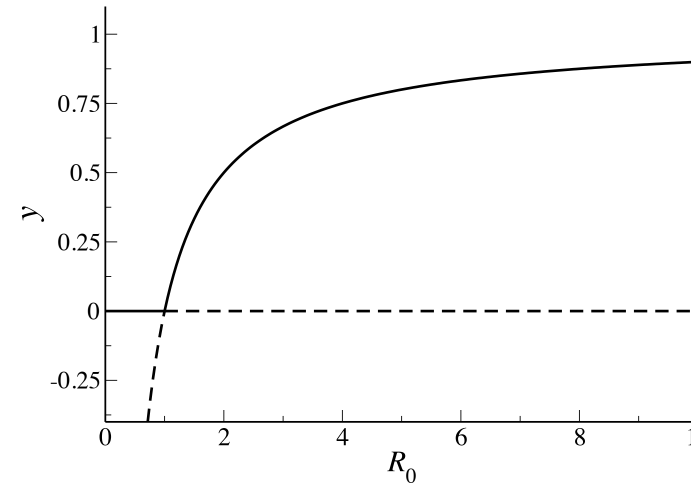
Qualitatively, the model behaves the same for all R_0 values less than one (infection free equilibrium is stable), and for all R_0 values greater than one (infection free equilibrium is unstable, endemic equilibrium exists and is stable)

***R_0* = 1 is a threshold condition**: below this value, infection can neither invade nor persist in the system; above this value, infection can invade and persist

Biological Interpretation and Implications

***R_0* = 1 is a threshold condition**: below this value, infection can neither invade nor persist in the system; above this value, infection can invade and persist

R_0 is known as the **basic reproductive number** and equals the **average number of secondary infections caused by a single infective individual in an otherwise entirely susceptible population**



The threshold condition makes sense:
If $R_0 > 1$, infectives give rise to more than one infection, and so disease can spread
If they give rise to less than one infection, disease cannot spread

Thinking about the parameters β and γ, the definition $\boldsymbol{R_0 = \beta/\gamma}$ makes sense:
higher transmission parameter: more infections. Higher recovery rate: fewer infections

R_0 measures the ability of the infection to spread

An Interlude: Non-Dimensionalization

The SIS model has three parameters, *N*, β and γ : $$\frac{dI}{dt} = \frac{\beta(N-I)I}{N} - \gamma I$$

but its qualitative behavior depends on a single parameter combination, $\boldsymbol{R_0 = \beta / \gamma}$

Why is this? Why (in some sense) are two parameters unimportant?

Population size doesn't affect the qualitative behavior of the model: we were able to rewrite in terms of **fractions** of the population

$$\frac{dy}{dt} = \beta\left(1-y\right)y - \gamma y$$

This corresponds to measuring the number of infectives relative to the population size, in other words, changing the units in which we measure the number of infectives

What about the other "unimportant" parameter?

Non-Dimensionalization

$$\frac{dy}{dt} = \beta(1-y)y - \gamma y$$

What about the other "unimportant" parameter?

The timescale on which the infection spreads does not change the qualitative behavior

This corresponds to changing the units in which we measure time

A natural choice measures time relative to the average duration of infectiousness (1/γ)

$$\frac{dy}{dt} = \gamma\left\{\frac{\beta}{\gamma}(1-y)y - y\right\} \qquad = \gamma\left\{R_0(1-y)y - y\right\}$$

$$\frac{dy}{d\tau} = R_0(1-y)y - y$$

τ is time measured in these new units, $\tau = t\,\gamma$

(This essentially corresponds to setting the average duration of infection equal to 1)

Non-dimensionalization: measuring state variables & time in different units (rescaling)

Because we have two quantities that we can rescale (*I* and *t*), we can reduce the number of parameters by two

Non-Dimensionalization

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For this course, I want you to be **aware** that you can non-dimensionalize; I won't ask you to non-dimensionalize a given model

Final comment: logistic growth model has two parameters, *r* and *K*

Can non-dimensionalize, measuring *N* in units of the carrying capacity and time in units of 1/*r*

Can show that this leaves us with a non-dimensionalized logistic growth model that has no parameters (!)

$$\frac{dy}{dt} = y\left(1 - y\right)$$

All logistic growth models (assuming *r* and *K* are both positive) share the same qualitative behavior (we have already seen this)

Transcritical (Exchange of Stability) Bifurcation

Algebraically, the simplest model that has a transcritical bifurcation is

$$\frac{dy}{dt} = y(a - y)$$

(Logistic growth, with carrying capacity *a*, where *a* can be positive, negative or zero
- although zero and negative values of *a* aren't biologically meaningful…)

See homework!

Saddle-Node Bifurcation

We saw this a couple of lectures ago, when we talked about the logistic growth model subject to harvesting at a constant rate:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - h$$

$h = 0$: logistic growth, unstable equilibrium at 0 and a stable equilibrium at K

As we look at larger values of h, the two equilibria move closer to each other

Eventually, there is a value of h at which the two equilibria collide

Beyond this, there are no equilibria

We saw all of this graphically, but we can also do the analysis using the algebraic approach

$$g(N) = rN\left(1 - \frac{N}{K}\right) - h$$

The algebra is straightforward, but slightly messy

Saddle-Node Bifurcation in Harvesting Model

Step 1: Find the equilibria. Solve $g(N) = 0$

$$0 = rN\left(1-\frac{N}{K}\right)-h \;\; = rN-\frac{rN^2}{K}-h \;\; = -\frac{rN^2}{K}+rN-h$$

Quadratic equation for *N*

$$0 = -\frac{rN^2}{K}+rN-h$$

Could use quadratic formula on this. But I prefer to rearrange to make the coefficient of N^2 equal to one

$$0 = \frac{-r}{K}\left\{N^2-KN+\frac{hK}{r}\right\}$$

$$0 = N^2-KN+\frac{hK}{r}$$

$$N = \frac{-B\pm\sqrt{B^2-4AC}}{2A}$$

$$A=1, \quad B=-K, \quad C=hK/r$$

$$N = \frac{K\pm\sqrt{K^2-4hK/r}}{2}$$

$$N = \frac{K}{2}\pm\frac{\sqrt{K^2-4hK/r}}{2}$$

Two solutions if $K^2-4hK/r>0$

one solution if $K^2-4hK/r=0$

no solutions if $K^2-4hK/r<0$

Saddle-Node Bifurcation in Harvesting Model

$$K^2 - 4hK/r = K\left(K - 4h/r\right)$$

K is positive, so $K^2 - 4hK/r > 0$ means $K - 4h/r > 0$

In other words, if $h < rK/4$ we have two equilibria

If $h = rK/4$ we have one equilibrium

If $h > rK/4$ we have no equilibria

This makes sense if we recall that the fastest growth rate of the logistic growth model is $rK/4$

This is the fastest rate at which the population can replenish itself, hence the fastest rate at which we can sustainably remove individuals

If we remove individuals at greater than this rate, the population will continually decrease in size

(Remember, this model has the unrealistic feature that N will go negative in this case.)

Saddle-Node Bifurcation in Harvesting Model

Step 2: Find the stability of the equilibria

$$g(N) = rN\left(1 - \frac{N}{K}\right) - h \;= -\frac{rN^2}{K} + rN - h$$

$$g'(N) = -\frac{2rN}{K} + r \quad = r\left(1 - \frac{2N}{K}\right)$$

We see that $g'(N) = 0$ if $N = K/2$, that $g'(N) < 0$ if $N > K/2$ and that $g'(N) > 0$ if $N < K/2$

Our equilibria are $N = \dfrac{K}{2} \pm \dfrac{\sqrt{K^2 - 4hK/r}}{2}$

These are symmetrically positioned about $K/2$, so the larger has $g'(N) < 0$ (stable) and the smaller has $g'(N) > 0$ (unstable)

When $h = rK/4$, the single equilibrium has $g'(N) = 0$; but a graphical analysis shows this to be semi-stable

Saddle-Node Bifurcation in Harvesting Model

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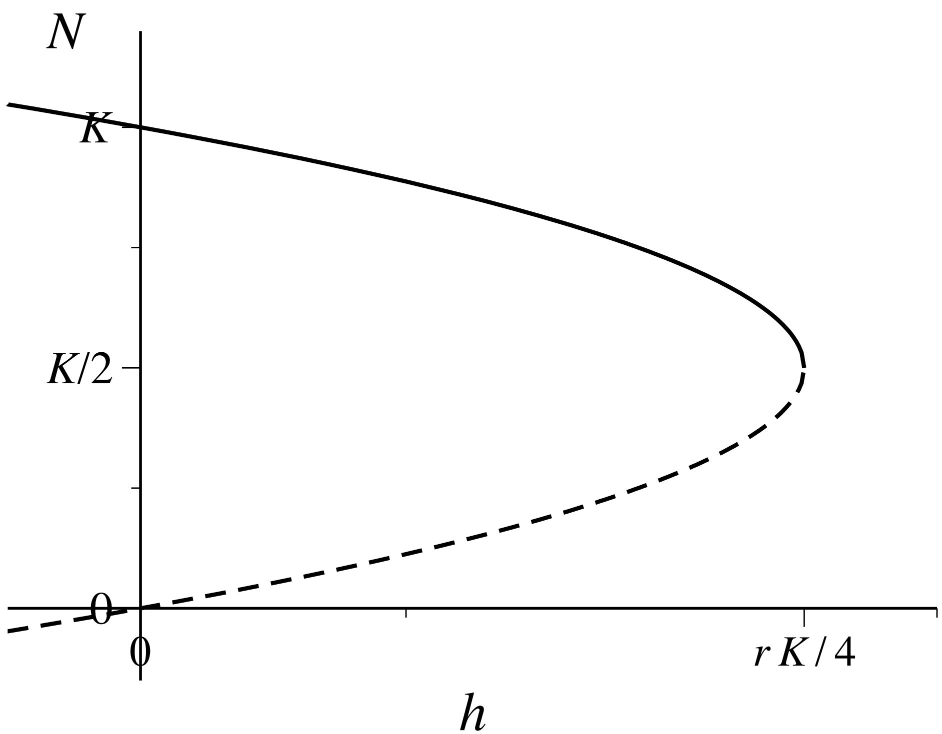
Saddle-Node Bifurcation in Harvesting Model

Bifurcation diagram for the logistic model with constant harvesting

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - h$$



Saddle node bifurcation when *h* = *rK*/4, as the two equilibria collide and destroy each other

Saddle-Node Bifurcation

Algebraically, the simplest model that has a saddle-node bifurcation is

$$\frac{dy}{dt} = a - y^2$$

See homework!