MA 331

Differential Equations for the Life Sciences

Fall 2018

Lecture 9

Bifurcations

Big question in this section: suppose we have a model that involves some parameter

How does the qualitative behavior of the model depend on that parameter?

Does the model behave similarly for some ranges of the parameter?

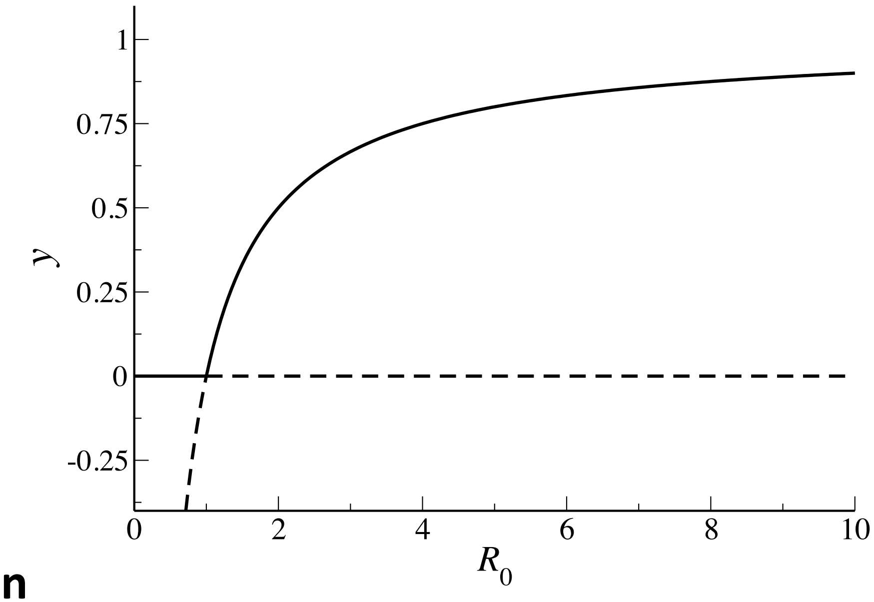
At what value(s) of the parameter does behavior change?

How does behavior change?
(e.g. does stability of an equilibrium change? Does the number of equilibria change?)

Bifurcation: a change in the qualitative behavior of a model at some value of a parameter

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

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

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

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

See homework!

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: multiply through by (-*K*/*r*)

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

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

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

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

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

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

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

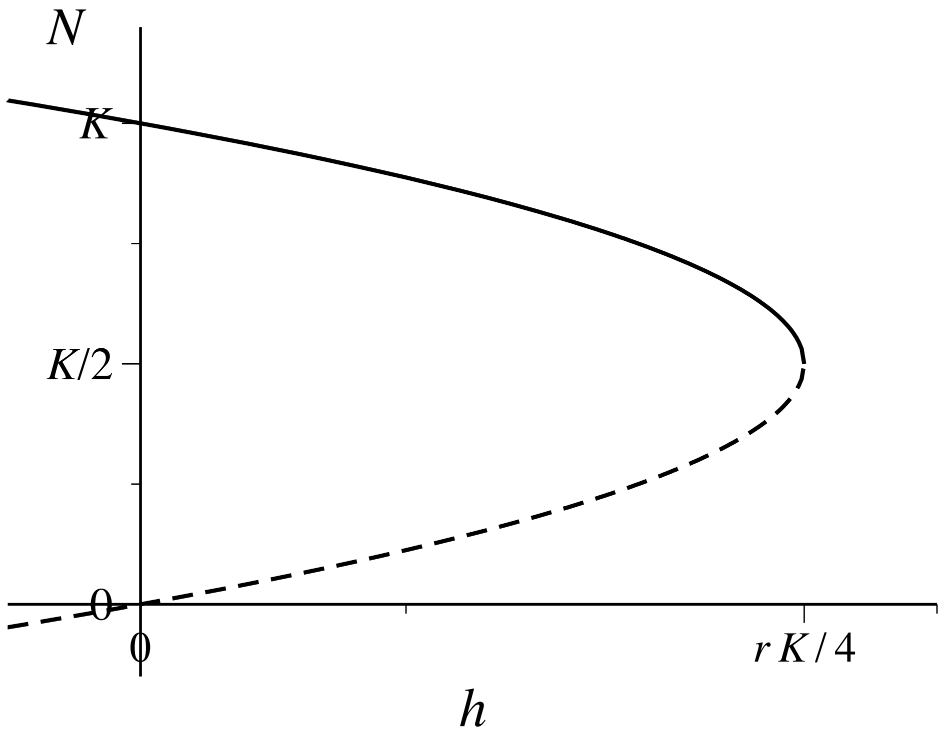
These are symmetrically positioned about $K/2$, so the larger has $g'(N) < 0$ (stable) and the smaller has $g'(N) > 0$ (unstable)

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

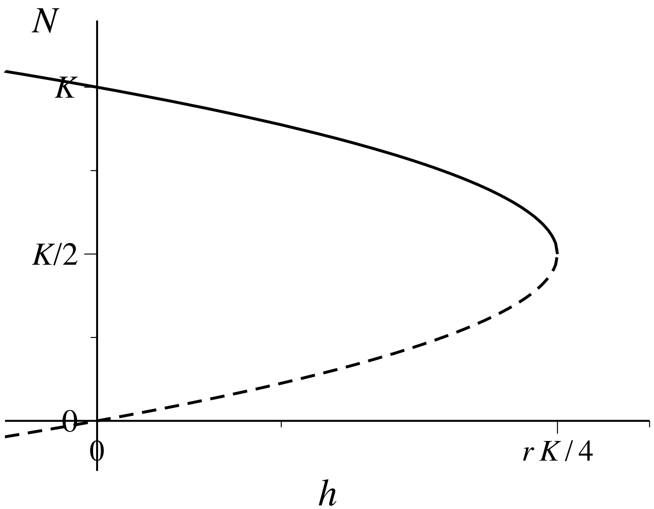
Bifurcation diagram for the logistic model with constant harvesting

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



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

Ecological Comments on Harvesting Model



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

Imagine that we start off with no harvesting, and population sitting at its carrying capacity

Then slowly increase harvesting. What will happen?

Population will track the upper curve (stable equilibrium): population size will decrease as harvesting increases

Everything will be OK until *h* reaches *rK*/4. Above this point there is no stable equilibrium, so population will suddenly crash

This behavior is clear from the bifurcation diagram, but imagine if all we could see was the population responding to increasing harvesting

Troubling aspect from an ecological viewpoint: there was no indication that population would crash in this way: as *h* was increased, *N* slowly decreased until we very suddenly "fell off the edge of the cliff" without warning "Tipping point"

A More Realistic Harvesting Model

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

We previously discussed why this model is unrealistic: it assumes that harvesting rate is constant, regardless of population size

Clearly we cannot harvest at rate *h* if the population size is zero!

A more realistic model would have the harvesting term depend on the population size *N*

Simplest description: assume that harvesting rate is proportional to *N* : hN

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

(By the way, the right hand side of this differential equation is fairly similar to that of the SIS model from last time…)

Equilibria? Solve $0 = rN\left(1-\frac{N}{K}\right)-hN$

$$0 = N\left\{r\left(1-\frac{N}{K}\right)-h\right\}$$

Either $N = 0$ or $N = K(1-h/r)$ Notice, 2nd equilibrium = 0 when $h = r$

A More Realistic Harvesting Model

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

Equilibria: Either $N = 0$ or $N = K(1\text{-}h/r)$

Stability? $g(N) = rN\left(1 - \frac{N}{K}\right) - hN \;\; = rN - \frac{r}{K}N^2 - hN$

$$g'(N) = r - \frac{2rN}{K} - h$$

$N = 0$: $\quad g'(0) = r - h$

$g'(0) > 0$ if $h < r$ *unstable*

$g'(0) < 0$ if $h > r$ *stable*

$N^* = K(1\text{-}h/r)$: $\quad g'\left(K\left(1 - h/r\right)\right) = r - \frac{2r}{K}K\left(1 - \frac{h}{r}\right) - h \;\; = r - 2r\left(1 - \frac{h}{r}\right) - h \;\; = -r + h$

$g'(N^*) < 0$ if $h < r$ *stable*

$g'(N^*) > 0$ if $h > r$ *unstable*

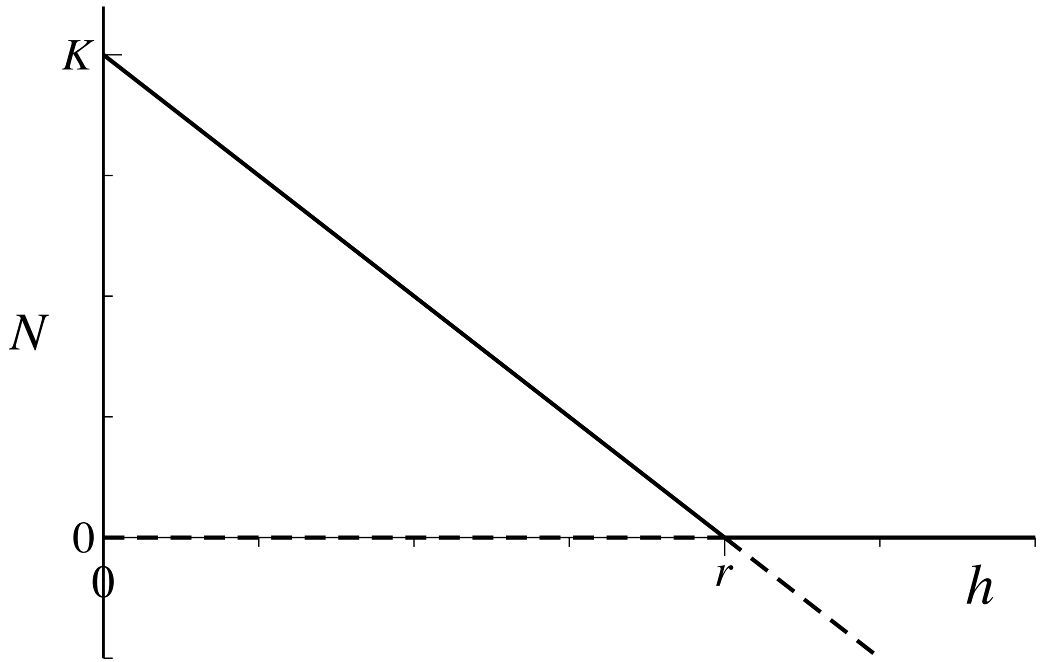
Equilibria collide when $h = r$ and exchange stability: transcritical bifurcation

A More Realistic Harvesting Model

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

Equilibria: Either $N = 0$ or $N = K(1\text{-}h/r)$

Bifurcation diagram:



Equilibria collide when $h = r$ and exchange stability: transcritical bifurcation

An Even More Realistic Harvesting Model

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

Harvesting term proportional to population size

In reality, there might be some limit to the amount of harvesting that can take place (e.g. a fishing fleet with a fixed number of ships)

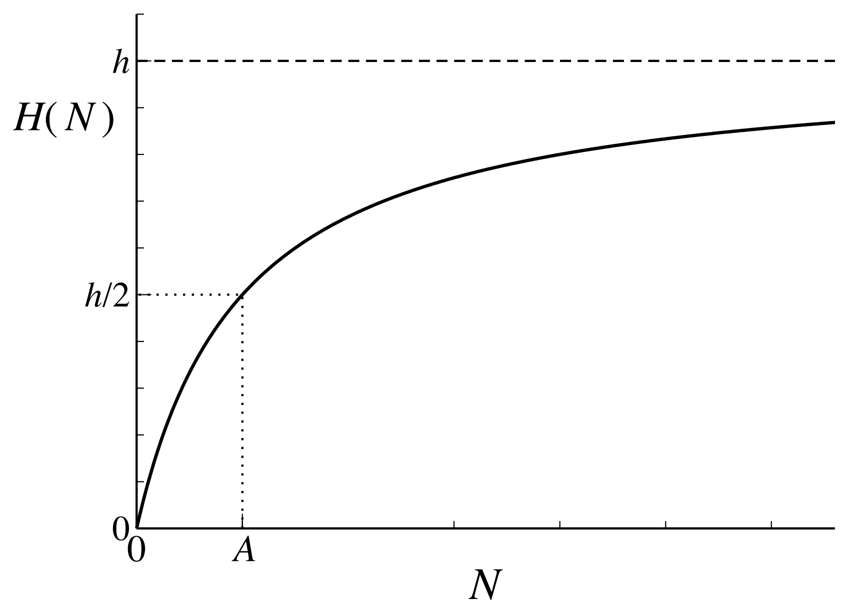
Saturating harvesting function: $H(N) = \dfrac{hN}{A + N}$

What does this look like?

When N is small, $A + N \approx A$,
and so $H(N) \approx hN/A$ (approx. linear)

When N is large, $A + N \approx N$,
and so $H(N) \approx hN/N \approx h$

When $N = A$, $H(N) = hA/(2A) = h/2$
"half maximum point"



An Even More Realistic Harvesting Model

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

Equilibria? $\quad 0 = rN\left(1-\frac{N}{K}\right) - \frac{hN}{A+N} \quad = N\left(r\left(1-\frac{N}{K}\right) - \frac{h}{A+N}\right)$

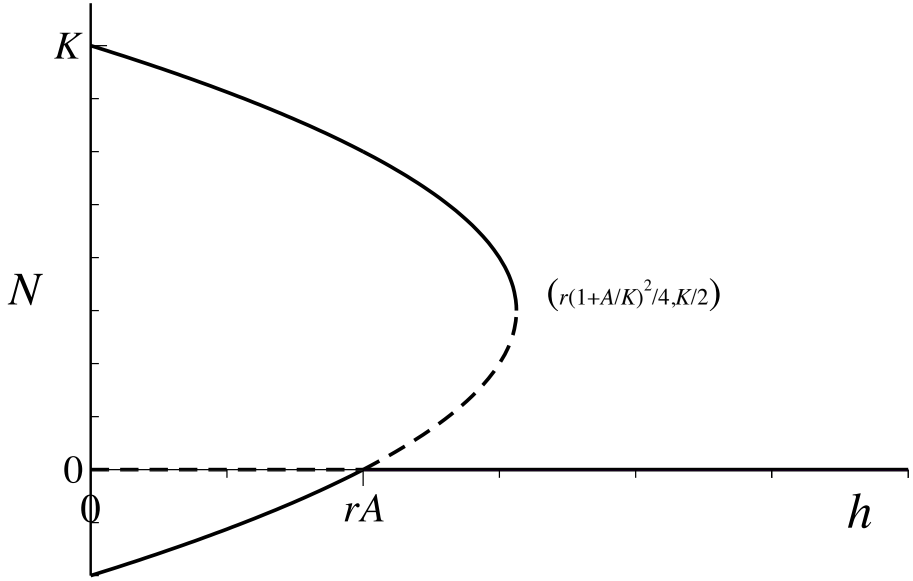
0 is always an equilibrium, and it's easy to show that (   ) = 0 gives rise to a quadratic equation, with 2, 1 or 0 solutions

An Even More Realistic Harvesting Model

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

Equilibria? 0 is always an equilibrium, plus an additional 2, 1 or 0 solution(s)

Can do the stability analysis (we skip the details) and get the following bifurcation diagram:



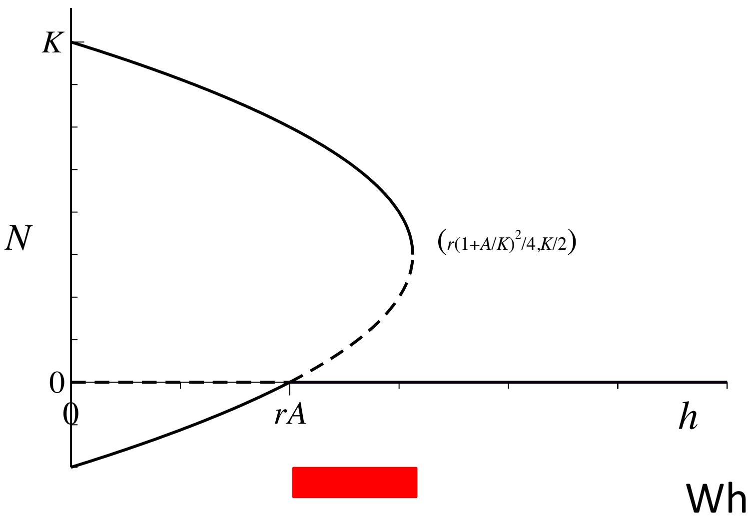
Equilibrium at 0 is unstable for small *h*, but stable for *h* > *rA*

Two other equilibria: one undergroes a transcritical bifurcation, at *h* = *rA* , with the equilibrium at 0

The two other equilibria undergo a saddle-node bifurcation at the value of *h* shown

An Even More Realistic Harvesting Model

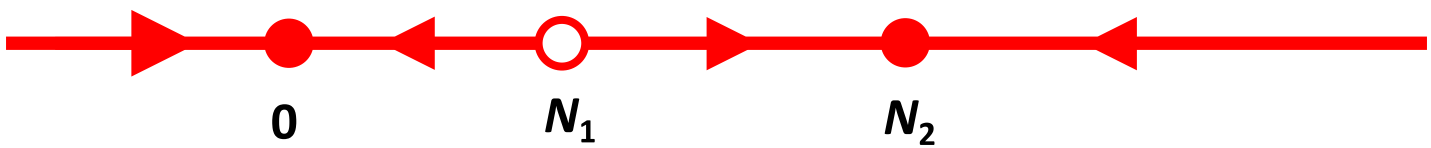
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{hN}{A+N}$$



This model exhibits the tipping point phenomenon: sudden disappearance of the positive stable equil. as harvesting is increased beyond some point

For a range of *h* values, shown by the red bar, the model has two stable biologically feasible equilibria: **bistability**

What does the phase diagram look like in the bistable region?

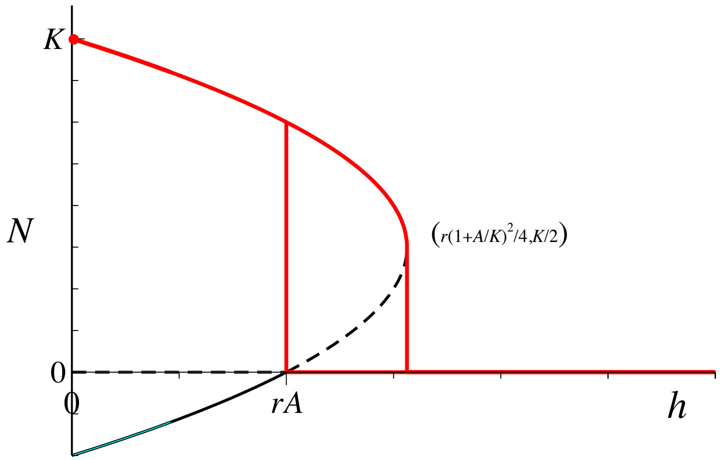


Stable equilibrium at 0, positive stable equilibrium and an unstable equilibrium in between

Which equilibrium is approached in the long run depends on the initial condition:
start below the unstable equilibrium and arrows take you to zero
start above the unstable equilibrium, arrows take you to the positive stable equilibrium

Two **basins of attraction**: initial conditions in $(-\infty, N_1)$ go to 0, those in $(N_1, -\infty)$ go to N_2
The point N_1 separates these two (“separatrix”: think “continental divide”)

Ecological Comments; Hysteresis



This model exhibits the tipping point phenomenon: sudden disappearance of the positive stable equilibrium as harvesting is increased beyond some point

For a range of *h* values, the model has two stable biologically feasible equilibria: **bistability**

Bistability can lead to some very interesting behavior:

Imagine starting off at *h* = 0, with population sitting at its carrying capacity

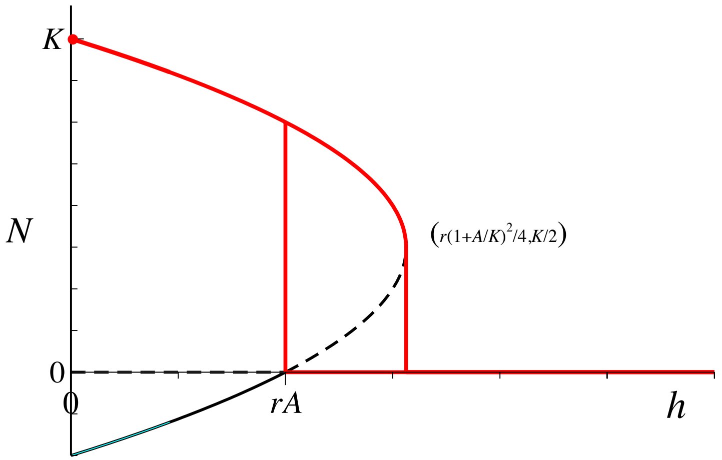
As *h* is increased, population will slowly decrease until it falls off the edge of the cliff & goes extinct

What happens if you then decrease *h* and there is a small trickle of individuals into the population?

If you are above *h = rA,* population will stay at zero: it can only jump back up to positive stable equilibrium if you reintroduce enough individuals to overcome the lower unstable equilibrium

Once you are below *h = rA,* reseeding the population with some small number will cause it to jump back up to the positive stable equilibrium

Ecological Comments; Hysteresis



Important ecological message in this model:
Cannot undo the catastrophic effect of over-harvesting by simply reducing harvesting to what would have been a sustainable level

Hysteresis: when a change isn't reversed when you undo the change you made to the parameter