EEB 200B: Lloyd-Smith PS 1

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Question 1

The logistic model of density density dependence assumes that the per capita growth rate of the population decreases linearly with increasing N. However, it is not necessarily true that per capita growth rates deecrease monotonically with N. Under some circumstances per capita growth rates may increase with N at very low densities, then decrease as densities become higher. This phenomenon is called the Allee effect. The following equation describes a continuous time population model with an Allee effect combined with logistic density dependance:

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

Part A: Find all equilibrium points of this model.

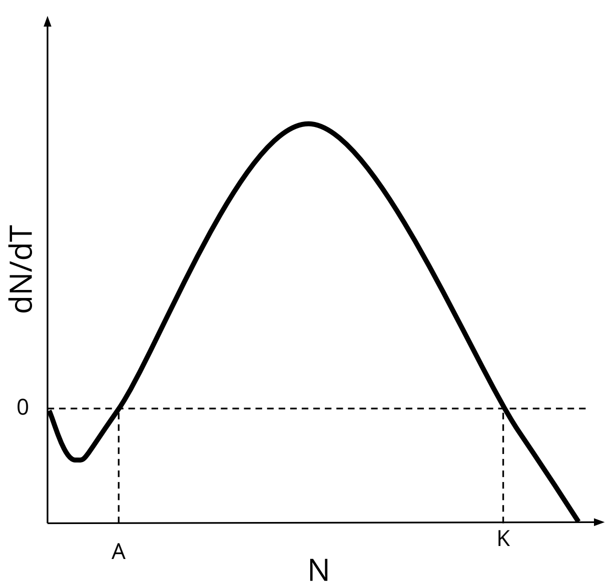
Equilibrium points occur where $\frac{dN}{dT} = 0$. This can happen in three ways:

$N = 0$

$N/K = 1$, in other words, $N = K$

$N/A = 1$, in other words, $N = A$

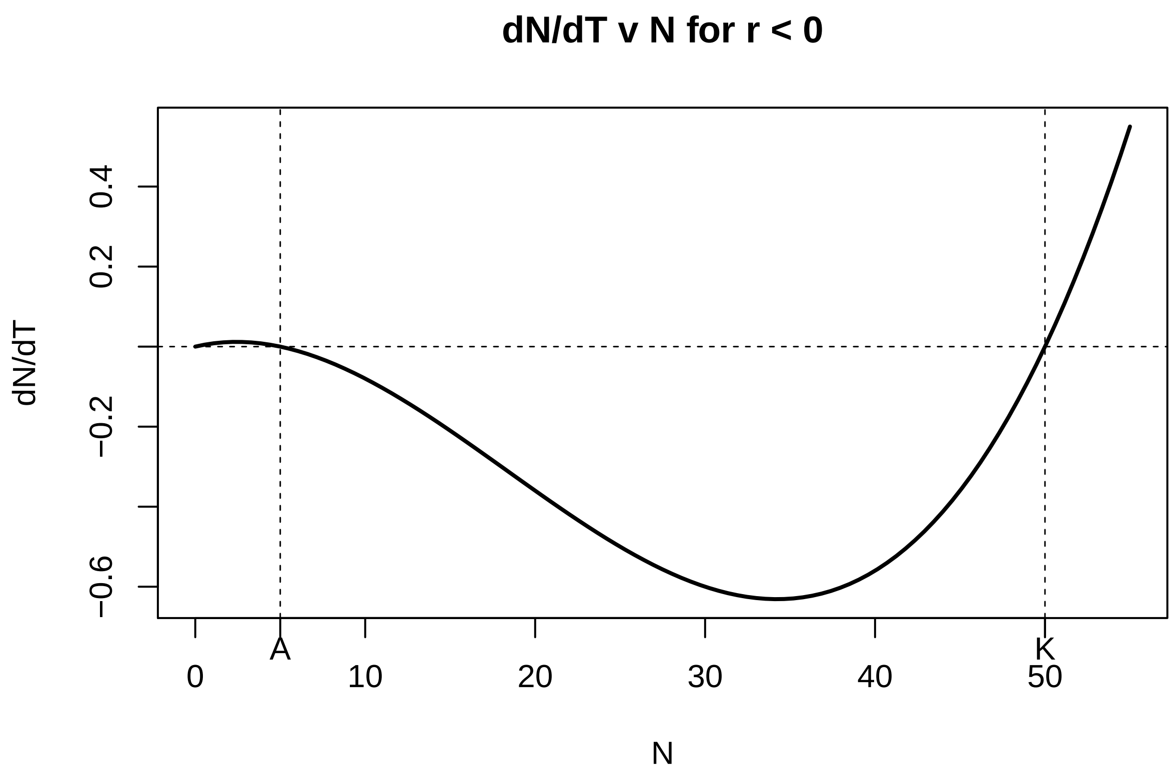
Part B: Sketch the population growth rate dN/dT as a function of N for $r > 0$. Predict stability of the equilibria.



Based on the slope of the curve as it passes through equilibrium points, I expect $N = 0$ to be a **stable** equilibrium, $N = A$ to be an **unstable** equilibrium, and $N = K$ to be a **stable** equilibrium.

Part C: Use `R` to plot the population growth rate dN/dT as a function of N for $r < 0$. Mark the stability of the equilibria.

```
# Define parameters
r <- -0.01
K = 50
A = 5

# use curve to plot dN/dT vs N
curve(r*x*(1-x/K)*((x/A)-1), from = 0, to = 55,
      xlab = "N", ylab = "dN/dT", lwd = 2,
      main = "dN/dT v N for r < 0")
# Add lines for dN/dT = 0, N = A, N = K
abline(h = 0, lty = 2, lwd = 0.75)
abline(v = A, lty = 2, lwd = 0.75)
abline(v = K, lty = 2, lwd = 0.75)
axis(side = 1, labels = c("A","K"), at = c(A, K), padj = -1.2)
```



Equilibrium point $N = 0$ is unstable; $N = A$ is a stable equilibrium, and $N = K$ is an unstable equilibrium.

Part D: Confirm predictions for $r > 0$ using local stabilty analysis

Step 1: Differentiate $f(N)$ with respect to N to obtain df/dN

$$\frac{dN}{dT} = (rN)(1 - \frac{N}{K})(\frac{N}{A} - 1)$$

$$= (rN - \frac{rN^2}{K})(\frac{N}{A} - 1)$$

$$= \frac{rN^2}{A} - rN - \frac{rN^3}{AK} + \frac{rN^2}{K} = \frac{dN}{dT}$$

Now, take the derivative:

$$\frac{df}{dN} = \frac{2r}{A}N - r - \frac{3r}{AK}N^2 + \frac{2r}{K}N$$

Step 2: Replace every instance of N in the derivative with the equilibrium value $\hat{N}$ to obtain $\left.\frac{df}{dN}\right|_{N=\hat{N}}$

First, assess this at equilibrium point $N = K$:

$$\left.\frac{2r}{A}N - r - \frac{3r}{AK}N^2 + \frac{2r}{K}N\right|_{N=K}$$

$$= \frac{2rK}{A} - r - \frac{3rK}{A} + 2r$$

$$= \frac{-rK}{A} + r$$

Given that $r > 0$ and $K > A$, the left (subtractive) component of the above equation is always a negative number with a larger absolute value than the right (additive) side; so, the *the value is always negative, and* ***the equilibrium is stable for the equilibrium point*** $N = K$***.***

Second, assess this at equilibrium point $N = A$:

$$\left.\frac{2r}{A}N - r - \frac{3r}{AK}N^2 + \frac{2r}{K}N\right|_{N=A}$$

$$= 2r - r - \frac{3rA}{A} + \frac{2rA}{K}$$

$$= r - \frac{rA}{K}$$

Given that $r > 0$ and $K > A$, the left (additive) side of the above equation is always a positive number with a larger absolute value than the right (subtractive) side; so, *the value is always positive, and* ***the equilibrium is unstable for the equilibrium point*** $N = A$***.***

Third, assess this at equilibrium point $N = 0$:

$$\left.\frac{2r}{A}N - r - \frac{3r}{AK}N^2 + \frac{2r}{K}N\right|_{N=0}$$

$$= -r$$

This number is always negative given $r > 0$, so ***the equilibrium point is stable for*** $N = 0$***.***

Part E: What does this mean for the fate of populations with $N < A$? How about for populations with $A < N < K$?

Populations with $N < A$ are predicted to shrink towards 0, whereas populations with $A < N < K$ are predicted to rise to K.

Part F: Describe three mechanisms that could give rise to Allee effects in a population.

Allee effects describe a rise in $\frac{dN}{Ndt}$, or per capita growth rates, at low values of N. Many biological drivers can cause an Allee effect:

- In populations of sexually reproducing organisms, individuals may be unable to find mates when the population is at a very low density. As density increases from very low to slightly higher, each individual may be more like to have a succesful mating- thus driving up the per capita growth rate. This mechanism can work in both animal and plant populations (e.g. the likelihood of a pollinator finding a conspecific may initially increase with population density).

- Populations of cooperative organisms might experience an Allee effect if, for example, individuals are unable to harvest enough food at low population densities. One can imagine a small wolf pack that is unable to kill any prey, and that the pack would fare better if it had more individuals to participate in the hunt. Similarly, a microbial population that acquires resources by secreting enzymes to break down molecules in the environment may be more efficient at resource acquisition at slightly higher population densities than at very low densities.
- There are bound to be more genetic problems in small populations than in larger populations- inbreeding among small populations can drive the expression of deleterious alleles, drift can drastically reduce variation, etc.

Question 2

Briefly describe the logic underlying local stability analysis for nonlinear population models. What is the role of Taylor expansion? What is the relation to linear models of population growth? Why is it "local" stability analysis?

In local stability analysis, we calculate the slope of dN/dT at or near an equilibrium point. When the slope is negative as the function dN/dT crosses 0, it means that the population is shrinking to the left of the equilibrium and growing to its right- in other words, it is moving away from the equilibrium point, which is therefore unstable. If the slope of dN/dT is positive as the function crosses 0, it means that the population is growing to the left, and shrinking to the right of the equilibrium point- in other words, it is converging on the point from both sides.

Taylor expansion helps us approximate the slope of the curve near a given point - here, the equilibrium point. We then can use the logic above to determine the stability of the equilibrium.

This analysis is called "local" because we an only assess the stability of a single equilibrium point at a time. A model can produce multiple equilibria- the Allee effect model in Q1, for example, has 3. The slope of dN/dT at each equilibrium point needs to be estimated separately to make predictions about that point.

Question 3

Consider two discrete time models for population dynamics:

- The Beverton-Holt model:

$$N_{t+1} = \frac{RN_t}{1 + [(R-1)/K]N_t}, R, K > 0$$

- The Ricker model:

$$N_{t+1} = N_t \ \exp \ \left[R\left(1 - \frac{N_t}{K}\right)\right], K > 0$$

Part A: Find all equilibrium points

At equilibrium, population size is not changing, so that $N_{t+1} = N_t$. We can solve both models for when this happens:

Beverton-Holt model:

$$\begin{aligned} N_{t+1} = N_t &= \frac{RN_t}{1 + [(R-1)/K]N_t}, R, K > 0 \\ 1 &= \frac{R}{1 + [(R-1)/K]N_t} \\ R &= 1 + [(R-1)/K]N_t \\ R - 1 &= \frac{R-1}{K}N_t \\ N_t &= K \end{aligned}$$

A second equilibrium point occurs where $N_t = 0$.

Ricker model:

$$\begin{aligned} N_{t+1} = N_t = N_t \ \exp \ &\left[R\left(1 - \frac{N_t}{K}\right)\right], K > 0 \\ 1 = \ \exp \ &[R(1 - \frac{N_t}{K})], K > 0 \\ ln(1) = ln(&\exp \ [R(1 - \frac{N_t}{K})]) \\ 0 = &R(1 - \frac{N_t}{K}) \\ 1 = &\frac{N_t}{K} \\ N_t = &K \end{aligned}$$

As above, a second equilibrium point occurs where $N_t = 0$.

Part B: Calculate local stability criteria for each equilibrium point. Over what ranges of R is each equilibrium point stable or unstable? Also specify ranges where N will oscillate.

First, ***local stability analysis for the Beverton-Holt Model***:

We first derive the Beverton-Holt model with respect to N (see end of document for steps) and then evaluate at $N = K$ and $N = 0$:

$$\frac{d}{dN} = \frac{K^2 R}{(K + (R-1)N)^2}\Bigg|_{N=0;N=K}$$

Equilibrium point	R	λ	behaviour
$N = 0$	(0, 1)	$0 < \lambda < 1$	stable, nonoscillatory
$N = 0$	(1,∞)	$\lambda > 1$	unstable, nonoscillatory
$N = K$	(0, 1)	$\lambda > 1$	unstable, nonoscillatory
$N = K$	(1,∞)	$1 < \lambda < 0$	stable, nonoscillatory

Second, ***local stability analysis for the Ricker Model***:

We first derive the Ricker model with respect to N (see end of document for steps) and evaluate at $N = K$:

$$\frac{d}{dN} = exp\left(R\left(1 - \frac{N_t}{K}\right)\right) * \left(1 - \frac{RN_t}{K}\right)\Bigg|_{N=0;N=K}$$

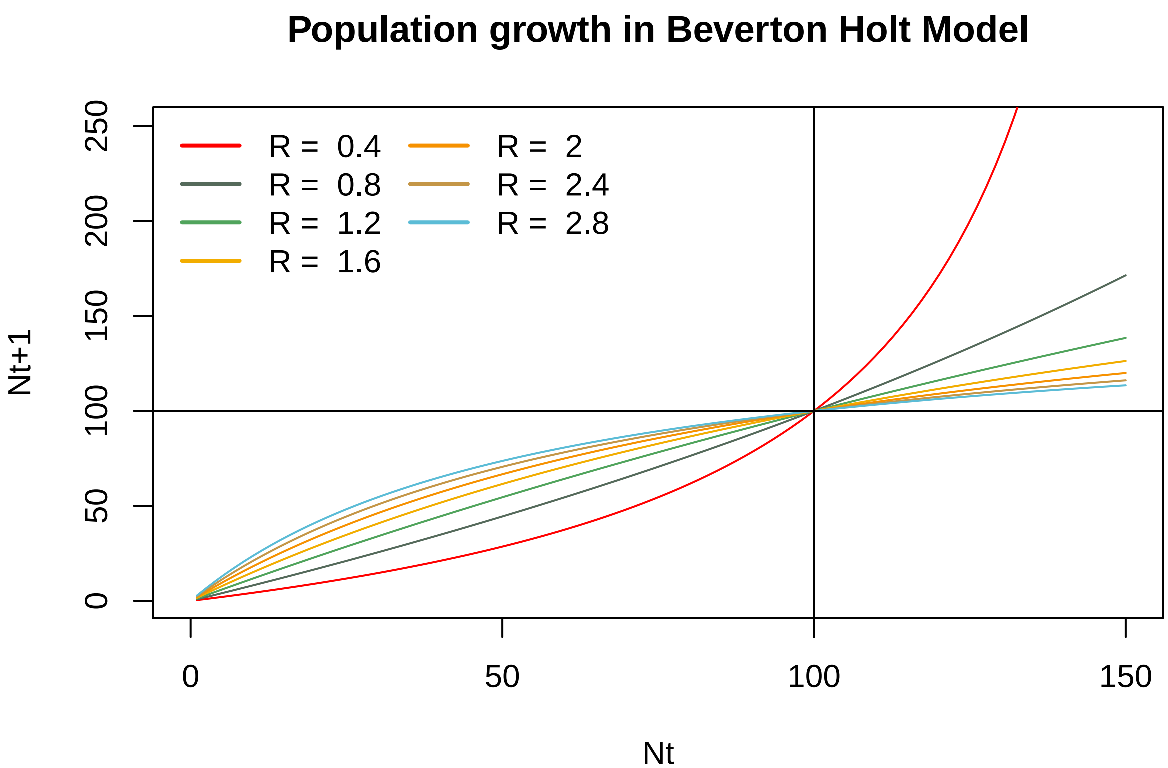
By substituting in values of R, we can develop the following:

Equilibrium point	R	λ	behaviour
$N = 0$	(-∞,0)	$0 < \lambda < 1$	stable, nonoscillatory
$N = 0$	(0, ∞)	$\lambda > 1$	unstable, nonoscillatory
$N = K$	(-∞,0)	$\lambda > 1$	unstable, nonoscillatory
$N = K$	(0,1)	$0 < \lambda < 1$	stable, nonoscillatory
$N = K$	(1,2)	-1 $< \lambda <$ 0	stable, oscillatory
$N = K$	(2,∞)	$\lambda <$ -2	unstable, oscillatory

Part C: Assume $K = 100$. Use `R` to plot N_{t+1} vs N_t for a range of values of R. Based on these plots, can the model display undamped oscillations or chaotic dynamics for any values of R? Why/not?

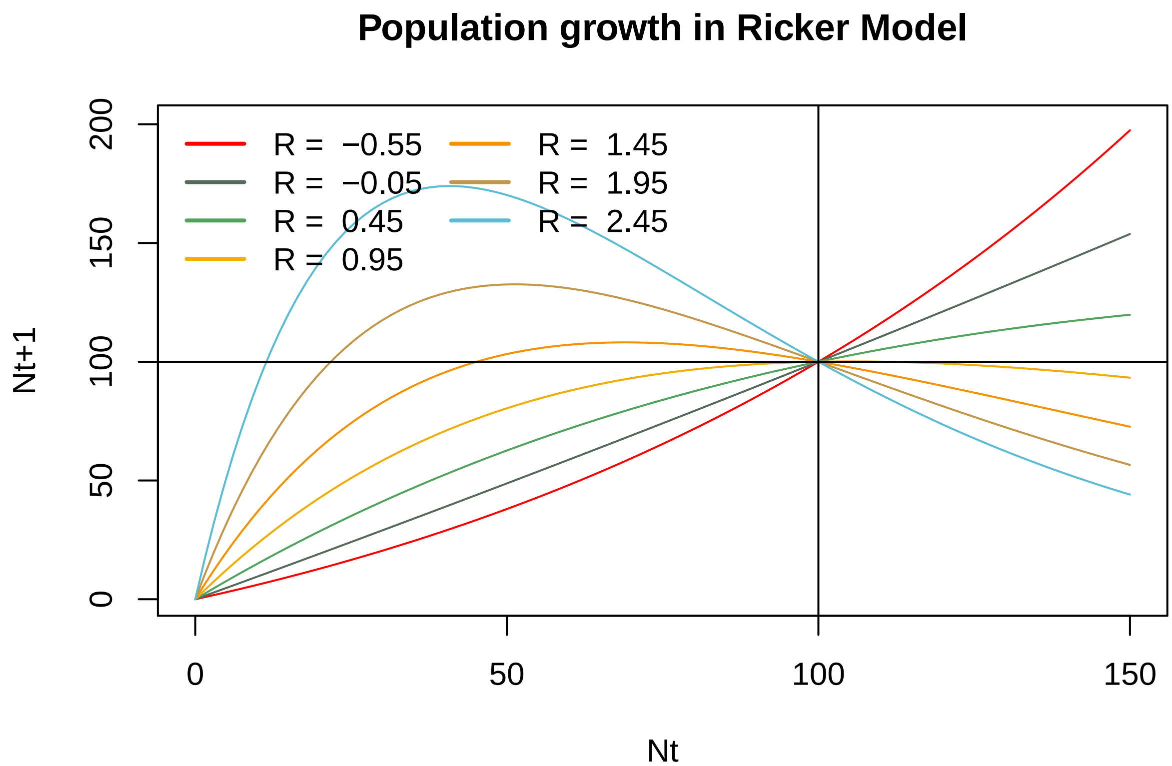
```
# Make a vector of Rs and define K = 100
Rs = seq(from = 0.4, to = 3, by = 0.4)
K = 100
# First, plot for Beverton-Holt Model
plot(1, type = "n",  xlab = "Nt", ylab = "Nt+1",
     main = "Population growth in Beverton Holt Model",
     xlim = c(0, 150), ylim = c(1, 250))
colors <- wesanderson::wes_palette("Darjeeling", n = length(Rs), type = "continuous")
for(ii in 1:length(Rs)) {
```

```
  curve((Rs[ii]*x)/(1+((Rs[ii]-1)/K)*x), from = 1, to = 150, add = T, col = colors[ii])
}
legend("topleft", lwd = 2, lty = 1, bty = "n",
       legend = paste("R = ", Rs), col = colors, ncol = 2)
abline(h = 100)
abline(v = 100)
```



This model is unlikely to show chaotic behavior or undamped oscillations- cobwebbing of the N_{t+1} v N_t graph suggests that the model will move unidirectionally. One intuition here might be that the N_{t+1} does not exceed K before N_t does- so that chances for oscillation above and below K seems unlikely in this model.

```
# Second, plot for Ricker model
Rs = seq(from = -0.55, to = 2.6, by = 0.5)
K = 100
plot(1, type = "n",  xlab = "Nt", ylab = "Nt+1",
     main = "Population growth in Ricker Model",
     xlim = c(0, 150), ylim = c(1, 200))
colors <- wesanderson::wes_palette("Darjeeling", n = length(Rs), type = "continuous")
for(ii in 1:length(Rs)){
  curve(x*(exp(Rs[ii]*(1-x/K))), from = 0, to = 150, add = T, col = colors[ii])
}
legend("topleft", lwd = 2, lty = 1, bty = "n",
       legend = paste("R = ", Rs), col = colors, ncol = 2)
abline(h = 100)
abline(v = 100)
```

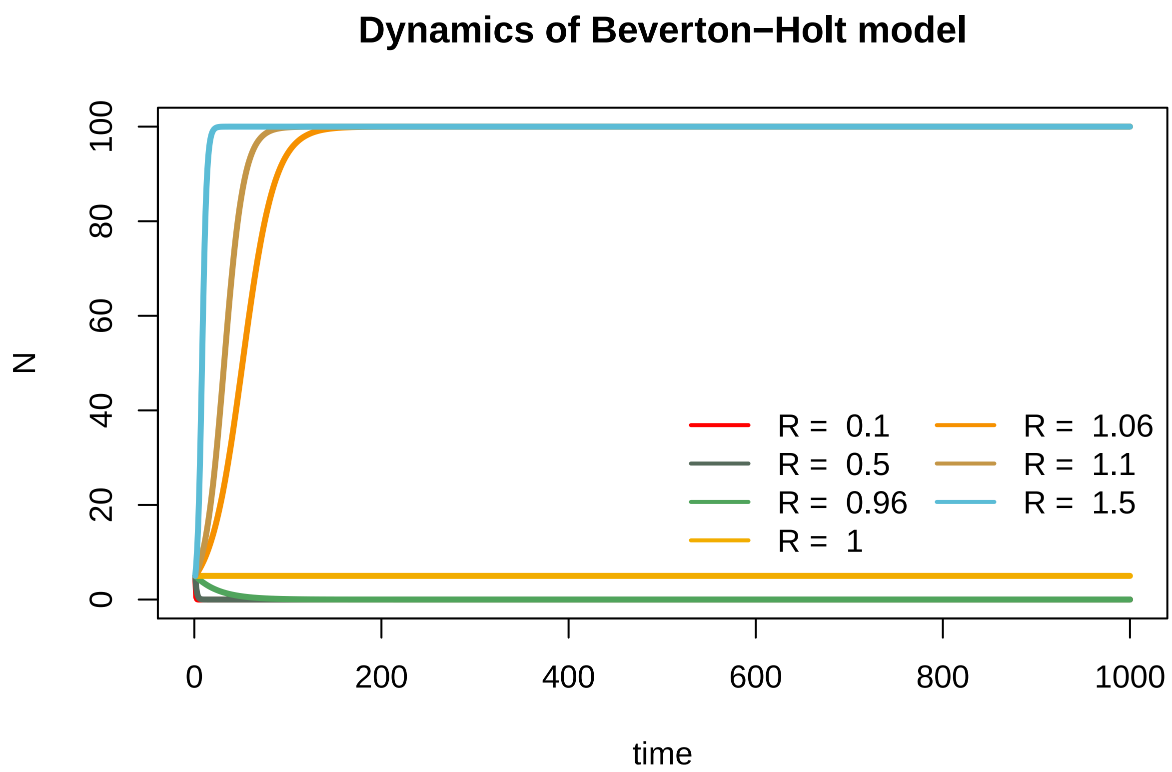


Chaotic behaviour and undamped oscillations are likely to arise in the Ricker model at high values of R- cobwebbing suggests that the populations will switch from being above and below K for sufficiently high Rs.

Part D: Write a script to simulate dynamics of the model (i.e. N_t vs t). For the largest equilibrium point (i.e. highest N^*) use simulations to verify the results of local stability analyses. Explore different values of R to test predictions about whether chaos is possible. If chaotic, demonstrate extreme sensitivity to initial conditions by differeing N_0 by tiny bits. Contrast the chaotic model to ones where the dynamics are stable.

```
# First, Beverton-Holt
bevholt <- function(R = 1, N0 = 5, K = 100, t = 1000) {
  timesteps <- t
  Nt <- numeric(timesteps)
  Nt[1] <- N0
  for (i in 2:timesteps) {
    Nt[i] <- (R*Nt[i-1])/(1+((R-1)/K)*Nt[i-1])
  }
  return(Nt)
}

# Create a range of Rs- recall that all R > 0 in BevHolt model

Rs <- c(0.1, 0.5, 0.96, 1, 1.06, 1.1, 1.5)
bevholt_output <- sapply(Rs, function(x) bevholt(R = x))
colors <- wesanderson::wes_palette("Darjeeling", n = length(Rs), type = "c")
```

```r
matplot(bevholt_output, lty = 1, lwd = 3, type = "l", col = colors,
        main = "Dynamics of Beverton-Holt model",
        xlab = "time", ylab = "N")
legend(x = 500, y = 45, lty = 1, lwd = 2, legend = paste("R = ", Rs),
       col = colors, ncol = 2, bty = "n")
```

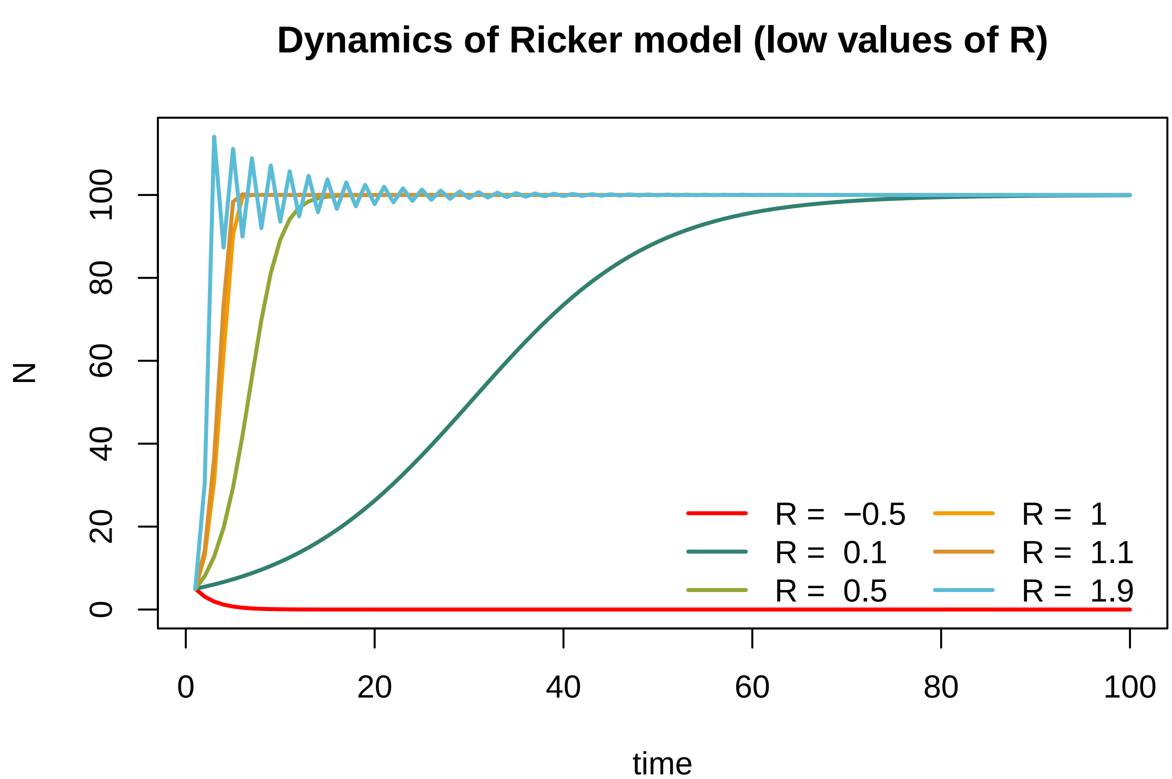


This graph confirms our predictions that unstable/oscillatory dynamics do not arise in the Beverton-Holt model- the trajectory of N is monotonic and tending towards K when $R > 1$ or towards 0 when $R < 1$.

We can repeat this exercise for the Ricker model:

```r
# Second, Ricker
ricker <- function(R = 1, N0 = 5, K = 100, t = 1000) {
  timesteps <- t
  Nt <- numeric(timesteps)
  Nt[1] <- N0
  for (i in 2:timesteps) {
    Nt[i] <- Nt[i-1]*exp(R*(1-(Nt[i-1]/K)))
  }
  return(Nt)
}

# Create a range of Rs from slightly below 1 to slightly above
```

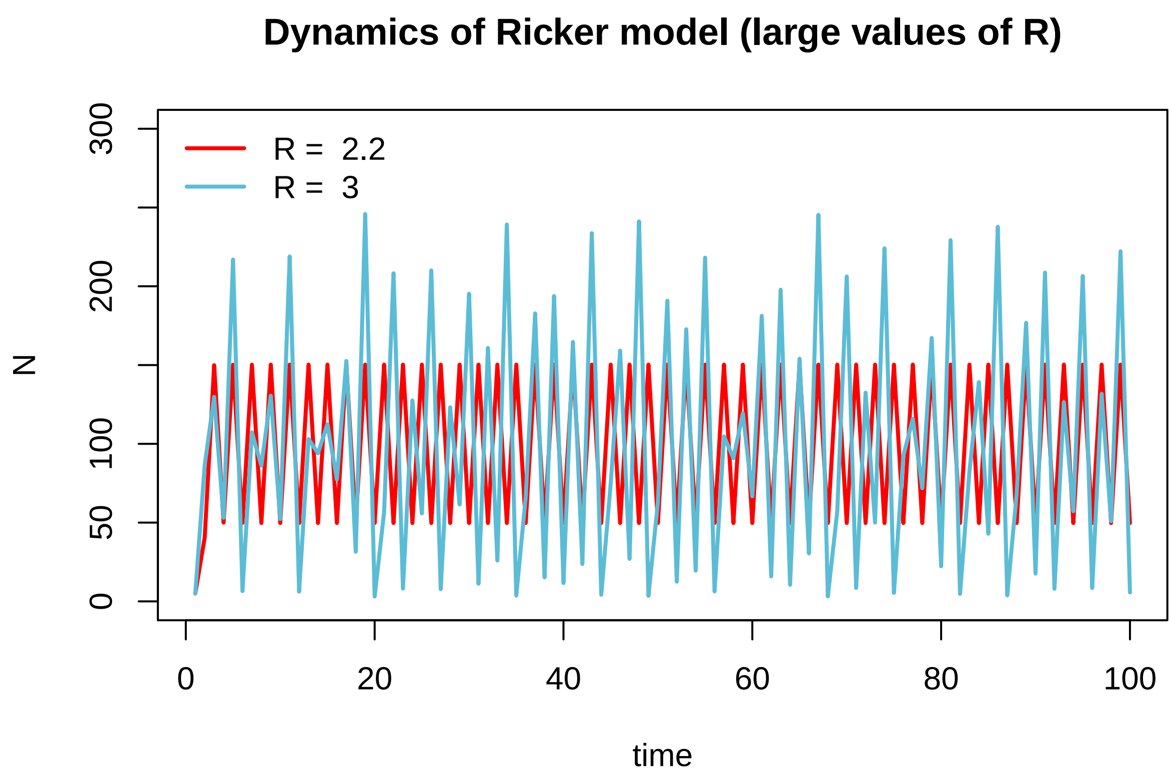
```
# I am going to put very high values of R on a separate graph
# Having them all on one makes things very messy!
Rs <- c(-0.5, 0.1, 0.5, 1, 1.1, 1.9)
ricker_output <- sapply(Rs, function(x) ricker(R = x, t = 100))
colors <- wesanderson::wes_palette("Darjeeling", n = length(Rs), type = "c")
matplot(ricker_output, lty = 1, lwd = 2, type = "l", col = colors,
        main = "Dynamics of Ricker model (low values of R)",
        xlab = "time", ylab = "N")
legend("bottomright", lty = 1, lwd = 2, bty = "n", col = colors, legend = paste("R = ", Rs), ncol = 2)
```



The graph above shows the dynamics of the Ricker Model with values of R ranging from 0.1 to 1.9- we see that for $R > 0$, all models converge to $N_t = K$. For $1 < R < 2$, we begin to see damped oscillations that converge onto K- this is most obvious for the line of $R = 1.9$, but is true of all $R > 1$.

Chaotic behaviour tends to arise when we use very large values of R. The answer to Q. 3B above suggests that at $R > 2$ the system will begin to assume unstable oscillatory dynamics. We can confirm this with simulation:

```
Rs <- c(2.2, 3)
ricker_output <- sapply(Rs, function(x) ricker(R = x, t = 100))
colors <- wesanderson::wes_palette("Darjeeling", n = length(Rs), type = "c")
matplot(ricker_output, lty = 1, lwd = 2, type = "l", col = colors,
        main = "Dynamics of Ricker model (large values of R)",
        ylim = c(0, 300), xlab = "time", ylab = "N")
legend("topleft", lty = 1, lwd = 2, bty = "n", col = colors, legend = paste("R = ", Rs))
```



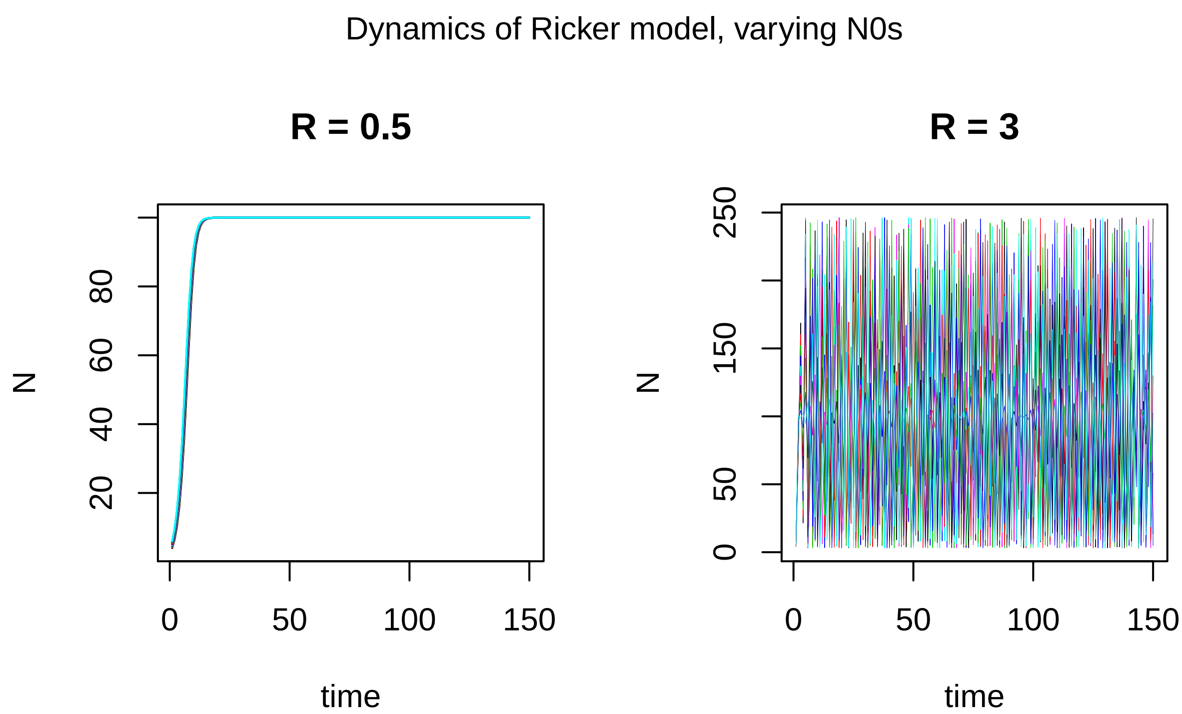
Now, we should demonstrate the impact of this chaotic behaviour by **varying the values of N_0 by small amounts**. I will do this by simulating dynamics for $R = 0.5$ and $R = 3$

```
N0s <- seq(from = 4, to = 6, by = 0.2)
ricker_stable <- sapply(N0s, function(x) ricker(R = 0.5, N0 = x, K = 100, t = 150))
ricker_chaos <- sapply(N0s, function(x) ricker(R = 3, N0 = x, K = 100, t = 150))

final_Ns <- cbind(N0s, ricker_stable[150, ], ricker_chaos[150, ])
colnames(final_Ns) <- c("$N_{0}$", "$N_{150}$ (R = 0.5)", "$N_{150}$ (R = 3)")
knitr::kable(final_Ns, align = "c")
```

N_0	N_{150} (R = 0.5)	N_{150} (R = 3)
4.0	100	200.800726
4.2	100	13.464729
4.4	100	102.499394
4.6	100	13.911643
4.8	100	14.674906
5.0	100	58.196913
5.2	100	245.522621
5.4	100	130.029495
5.6	100	181.522993
5.8	100	4.896807
6.0	100	213.984548

We can also show this in a plot:

```
par(mfrow = c(1,2), oma = c(0,0,4,0))
matplot(ricker_stable, type = "l", lty = 1, main = "R = 0.5", ylab = "N", xlab = "time")
matplot(ricker_chaos, type = "l", lty = 1, main= "R = 3", ylab = "N", xlab = "time", lwd = 0.25)
mtext(side = 3, "Dynamics of Ricker model, varying N0s", outer = T)
```

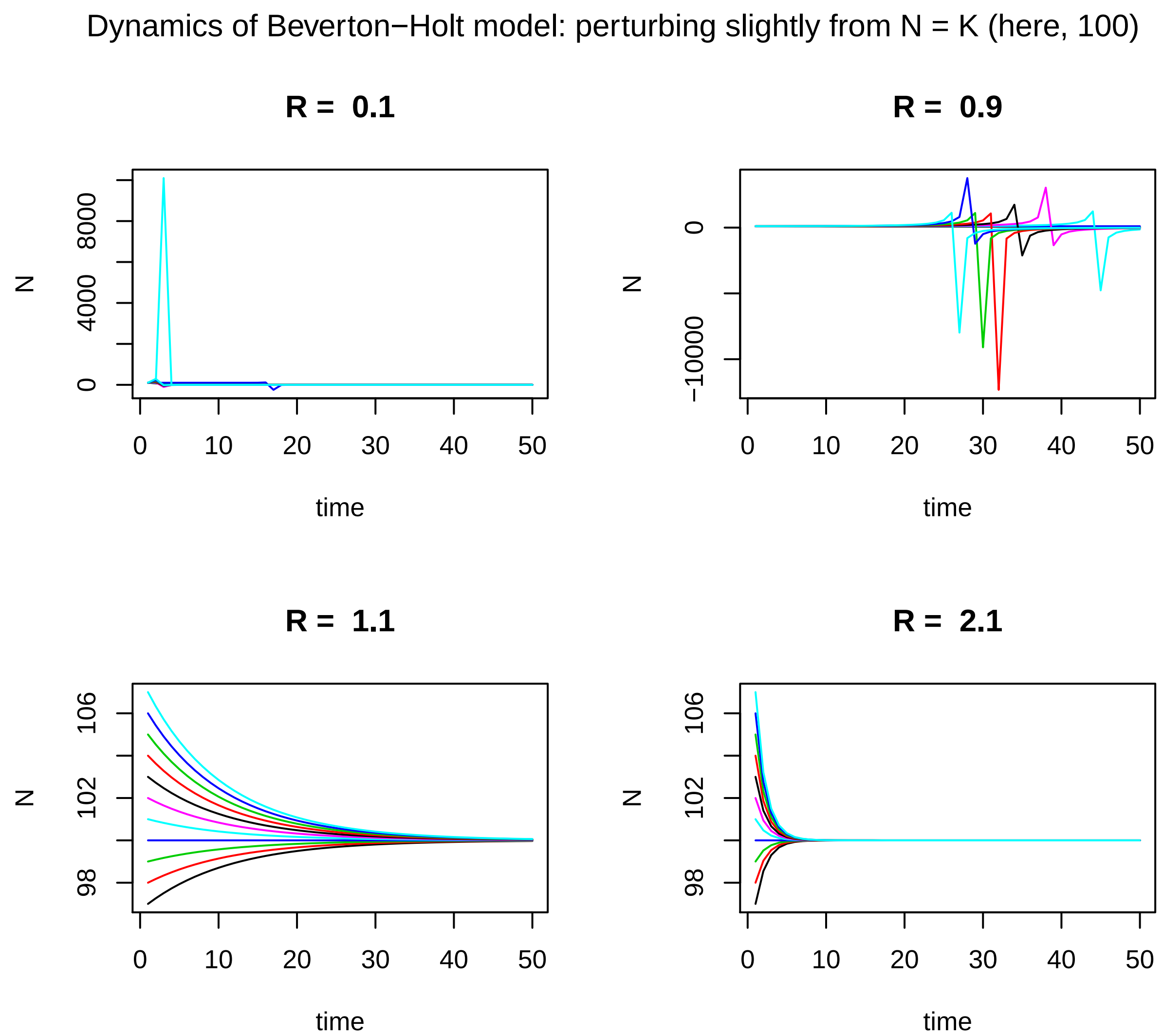


The graphs above show that slight variations in N_0 do not impact the trajectory of N or its stable value when $R < 2$ (in the "stable" region), but have a dramatic impact on the trajectory of N when $R > 2$ (in the "unstable" region.)

Now, we can demonstrate the stability of these models by **perturbing the system from $N = K$ to slight deviations**, and check if N returns to K.

First for the Beverton-Holt model:

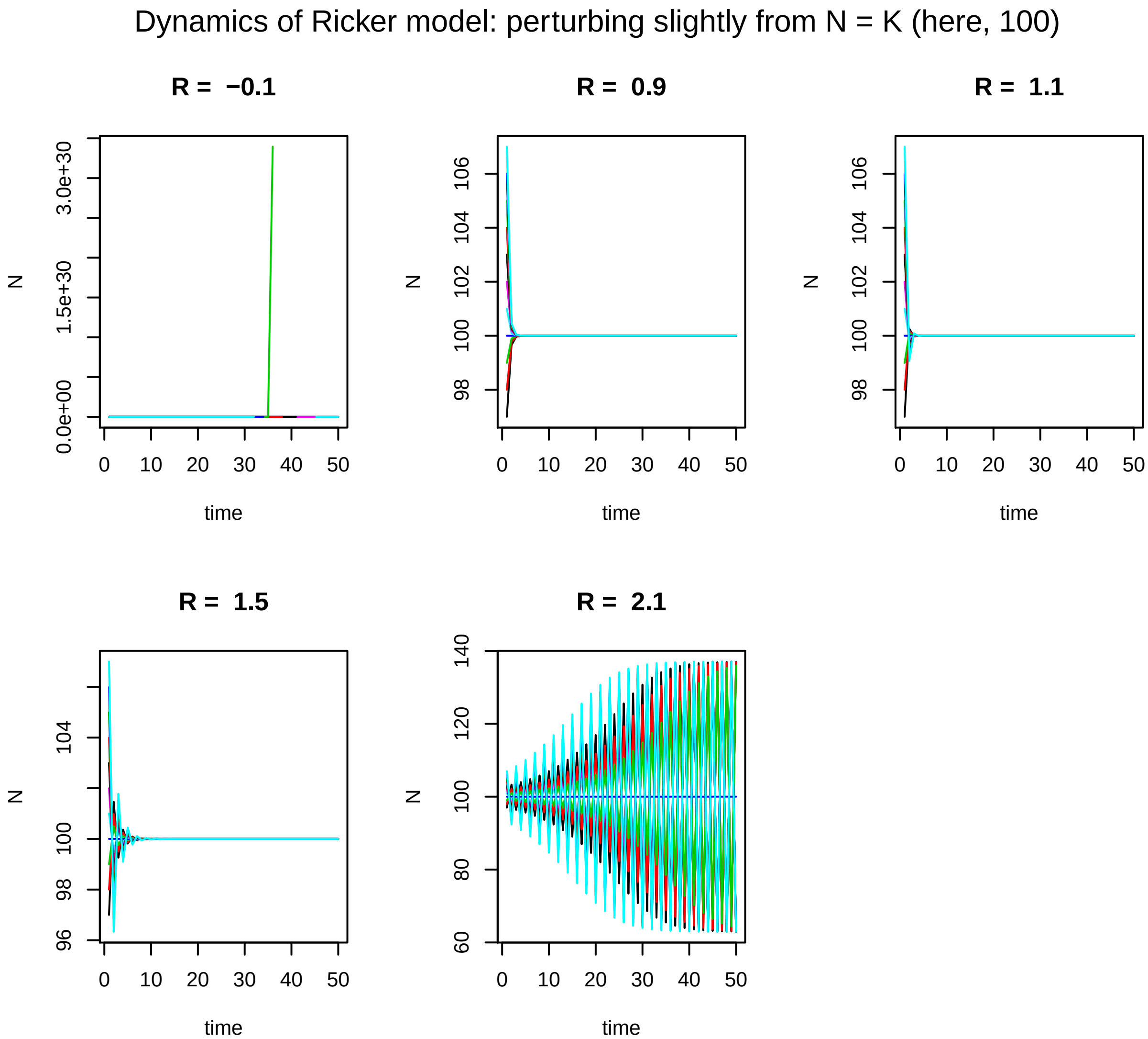
```
Ns <- seq(from = 97, to = 107)
par(mfrow = c(2,2), oma = c(0,0,3,0))
for(RR in c(0.1, 0.9, 1.1, 2.1)) {
  matplot(sapply(Ns, function(x) bevholt(R = RR, N0 = x, K = 100, t = 50)),
          type = "l", lty = 1, main = paste("R = ", RR), ylab = "N", xlab = "time")
}

mtext(side = 3, outer = T,
      text = "Dynamics of Beverton-Holt model: perturbing slightly from N = K (here, 100)")
```



These plots confirm that when $R > 1$ the model shows stable, non-oscillatory dynamics, and when $0 < R < 1$, it shows unstable, non-oscillatory dynamics.

And now, for the Ricker model:

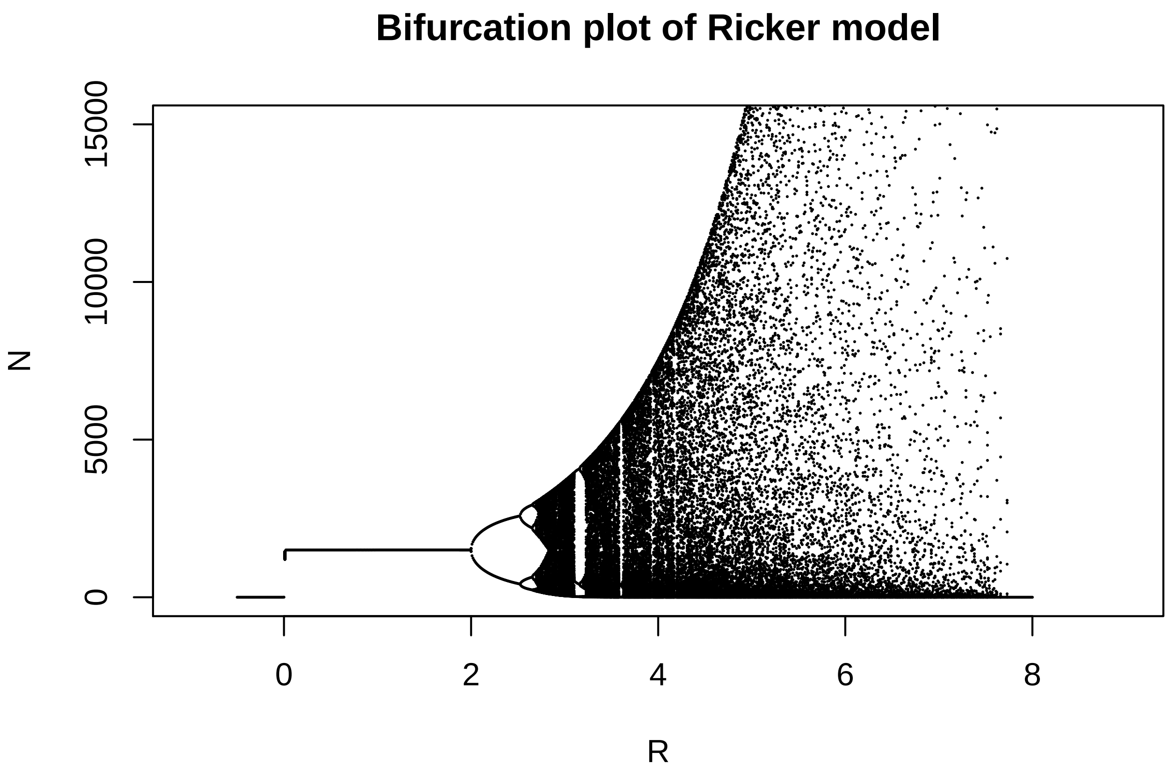
```
Ns <- seq(from = 97, to = 107)
par(mfrow = c(2,3), oma = c(0,0,3,0))
for (RR in c(-0.1, 0.9, 1.1, 1.5, 2.1)) {
  matplot(sapply(Ns, function(x) ricker(R = RR, N0 = x, K = 100, t = 50)),
          type = "l", lty = 1, main = paste("R = ", RR), ylab = "N", xlab = "time")
}
mtext(side = 3, outer = T,
      text = "Dynamics of Ricker model: perturbing slightly from N = K (here, 100)")
```



The plots confirm that when $R < 1$, the dynamics are stable and non-oscillatory, when $1 < R < 2$, the dynamics are stable and oscillatory, and when $R > 2$, the dynamics are unstable and oscillatory.

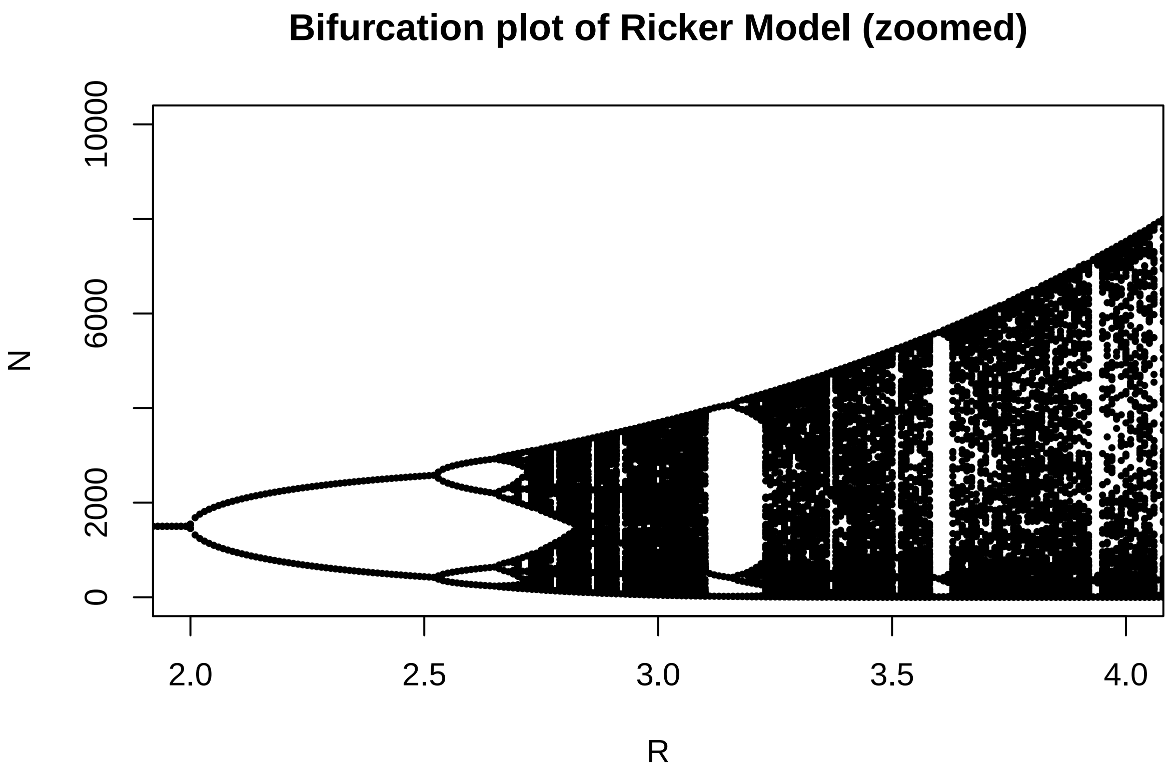
Part E: Use a computer to make a bifurcation plot showing the long term model dynamics over the interesting range of R. A bifurcation plot shows the stable states of the model as a function of R.

```
# Make a sequence of Rs- here from 0.5 to 8, by 0.01
Rs <- seq(from = -0.5, to = 8, by = 0.01)

# Calculate the trajectories of N for all Rs
trajectories <- sapply(Rs, function(x) ricker(R = x, N0 = 2, K = 1500, t = 1000))
# Floor the whole data frame - decimal values of N don't make sense
trajectories <- floor(trajectories)
# For each value of R, figure out how many UNIQUE values of N
# there are after 800 generations.
# If the system is stable, it should reach equilibrium by now
# and there should just be one unique value.
# If the system is unstable, it might have multiple values.
uniques <- apply(trajectories, 2, function(x) unique(x[800:1000]))

par(mfrow = c(1,1))
plot(1, type = "n", xlim = c(-1, 9), ylim = c(0, 15000), xlab = "R",
     ylab = "N", main = "Bifurcation plot of Ricker model")

# For each value of R, plot R on the X axis and the unique values
# of N on the Y axis
for(ii in 1:length(uniques)) {
  points(x = rep(Rs[ii], length(uniques[[ii]])), y = uniques[[ii]],
         pch = 16, cex = .2)
}
```



These bifurcation plots are predicted to be fractals- we can zoom in to confirm that it is a repeating pattern:

```
plot(1, type = "n", xlim = c(2, 4), ylim = c(0, 10000), xlab = "R",
     ylab = "N", main = "Bifurcation plot of Ricker Model (zoomed)")

for(ii in 1:length(uniques)) {
  points(x = rep(Rs[ii], length(uniques[[ii]])), y = uniques[[ii]],
         pch = 16, cex = .5)
}
```


Bifurcation plot of Ricker Model (zoomed)
N
0
2000
6000
10000
2.0
2.5
3.0
3.5
4.0
R

Deriving the Beverton-Holt and Ricker models To keep the main body clean, I have moved the steps in the derivatives of the two models here.

First, the Beverton-Holt Model:

$$\frac{d}{dN}\frac{RN_t}{1+[(R-1)/K]N_t}$$

$$= \frac{\frac{d}{dN}RN_t * 1+[(R-1)/K]N_t - RN_t * \frac{d}{dN}1+[(R-1)/K]N_t}{(1+[(R-1)/K]N_t)^2}$$

$$= \frac{R*(1+[(R-1)/K]N_t) - RN_t*[(R-1)/K]}{(1+[(R-1)/K]N_t)^2}$$

$$= \frac{R+[R*(R-1)/K]N_t - RN_t*[(R-1)/K]}{(1+[(R-1)/K]N_t)^2}$$

$$= \frac{R}{(1+[(R-1)/K]N_t)^2}$$

$$= \frac{R}{1+2N_t\frac{(R-1)}{K}+\left(\frac{(R-1)}{K}N_t\right)^2}$$

$$= \frac{R}{1+2N_t\frac{(R-1)}{K}+\left(\frac{(R-1)}{K}\right)^2 N_t^2}$$

$$= \frac{R}{1+2N_t\frac{(R-1)}{K}+\left(\frac{(R-1)^2}{K^2}\right) N_t^2}$$

$$= \frac{R}{\frac{K^2}{K^2}+\frac{2N_tK(R-1)}{K^2}+\left(\frac{(R-1)^2}{K^2}\right) N_t^2}$$

$$= \frac{RK^2}{K^2+2N_tK(R-1)+(R-1)^2N_t^2}$$

$$= \frac{RK^2}{[K+(R-1)N_t]^2}$$

Second, the Ricker model:

$$\frac{d}{dN} N_t * exp\left[R\left(1 - \frac{N_t}{K}\right)\right]$$

$$= \left(\frac{d}{dN} N_t\right) * exp\left[R\left(1 - \frac{N_t}{K}\right)\right] + N_t * \left[\frac{d}{dN} exp\left[R\left(1 - \frac{N_t}{K}\right)\right]\right]$$

$$= exp\left[R\left(1 - \frac{N_t}{K}\right)\right] + N_t * \left[\frac{d}{dN} exp\left(R - \frac{RN_t}{K}\right)\right]$$

$$= exp\left[R\left(1 - \frac{N_t}{K}\right)\right] + N_t * \left[\frac{d}{dN}\left(R - \frac{RN_t}{K}\right)\right] * exp\left[R\left(1 - \frac{N_t}{K}\right)\right]$$

$$= exp\left[R\left(1 - \frac{N_t}{K}\right)\right] + N_t * \left(0 - \frac{R}{K}\right) * exp\left[R\left(1 - \frac{N_t}{K}\right)\right]$$

$$= \left(1 - \frac{RN_t}{K}\right) * exp\left[R\left(1 - \frac{N_t}{K}\right)\right]$$