



Brown Bears versus Bald Eagles

*The Salmon Showdown during
Spawning Migration in Southeast Alaska's
temperate rainforests*

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Competition model: initial states and parameters

Resource: Salmon



Initial size: $R \Rightarrow 10,000$ individuals

Daily input upstream: Input $\Rightarrow 300$ salmon per day

Rate of input: $r_{in} \Rightarrow 1/300$ salmon per day

Carrying capacity: $K \Rightarrow 20,000$ individuals

Consumer 1: Brown Bears



Initial population size:

$C1 \Rightarrow 30$ bears

Birth rate per day

$\text{birth_rate_1} \leftarrow (2 \text{ cubs} / 2 \text{ adults}) / 365 \text{ days}$
(if 2 cubs per year survive to adulthood)

Death rate per day

$\text{death_rate_1} \leftarrow 1 / (20 \times 365)$
(bear lifespan: 20-25 years)

Consumer 2: Bald Eagles



Initial population size:

$C2 \Rightarrow 30$ eagles

Birth rate per day

$\text{birth_rate_2} \leftarrow (2 \text{ eaglets} / 2 \text{ adults}) / 365 \text{ days}$
(if 2 eagle babies survive to adulthood)

Death rate per day

$\text{death_rate_2} \leftarrow 1 / (15 \times 365)$
(eagle lifespan: 15-25 years)

Maximum consumption possible for each consumer

$C_{\text{max1}} \leftarrow 10$ salmons per day for 1 bear

$C_{\text{max2}} \leftarrow 3$ salmons per day for 1 eagle

Consumption required for each consumer per day as an essential resource during the season

$\text{consumption_1} \leftarrow 4$ (if 1 bear needs to eat 4 salmon per day)

$\text{consumption_2} \leftarrow 2$ (if 1 eagle needs to eat 2 salmon per day)

Reproductive efficiency for each consumer species per unit of resource consumed

$E1 \leftarrow \text{birth_rate_1} / (\text{consumption_1}) = 0.00068$ surviving cub per unit consumption

$E2 \leftarrow \text{birth_rate_2} / (\text{consumption_2}) = 0.00137$ surviving eaglet per unit consumption

Attack rates per day (unit: resource fraction caught by a consumer)

$\text{attack_rate_1} \leftarrow (\text{consumption_1}) / \text{input} = 0.013$ caught by a bear

$\text{attack_rate_2} \leftarrow (\text{consumption_2}) / \text{input} = 0.006$ caught by an eagle

Competition model: calculations



Rate of change of resource: Salmon

$$\frac{dR}{dt} = [r_{in} \times (K - R)] - [C_{max1} \times \frac{\text{attack rate 1} \times R}{C_{max1} + (\text{attack rate 1} \times R)} \times C1] - [C_{max2} \times \frac{\text{attack rate 2} \times R}{C_{max2} + (\text{attack rate 2} \times R)} \times C2]$$

$$\Rightarrow \frac{dR}{dt} = [\frac{1}{400} \times (20000 - 10000)] - [10 \times \frac{0.013 \times 10^4}{10 + (0.013 \times 10^4)} \times 30] - [3 \times \frac{0.0067 \times 10^4}{3 + (0.0067 \times 10^4)} \times 30]$$

$$\Rightarrow \frac{dR}{dt} = -339.7 \text{ salmon per day}$$

A decrease of 3.397% per day in the resource



Rate of change of consumer 1: Brown Bears

$$\frac{dC1}{dt} = [E1 \times C_{max1} \times \frac{\text{attack rate 1} \times R}{C_{max1} + (\text{attack rate 1} \times R)} - \text{death rate 1}] \times C1$$

$$\Rightarrow \frac{dC1}{dt} = [0.00068 \times 10 \times \frac{0.013 \times 10^4}{10 + (0.013 \times 10^4)} - 0.000137] \times 30 = 0.185 \text{ fraction of bear population per day}$$

An increase of 0.61% per day



Rate of change of consumer 2: Bald Eagles

$$\frac{dC2}{dt} = [E2 \times C_{max2} \times \frac{\text{attack rate 2} \times R}{C_{max2} + (\text{attack rate 2} \times R)} - \text{death rate 2}] \times C2$$

$$\Rightarrow \frac{dC2}{dt} = [0.00137 \times 3 \times \frac{0.067 \times 10^4}{3 + (0.067 \times 10^4)} - 0.0001826] \times 30 = 0.112 \text{ fraction of eagle population per day}$$

An increase of 0.37% per day

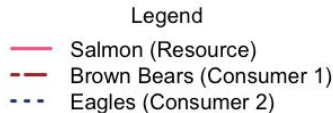
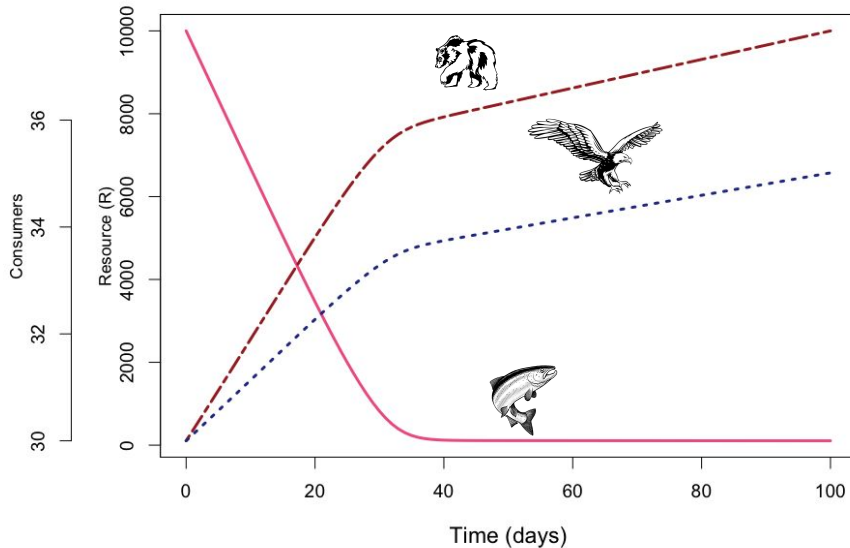
The initial growth rates for brown bears and bald eagles are quite different, and brown bears seem to be leading with an increase of 0.61% per day.

However, this does not mean that brown bears will necessarily prosper in steady state dynamics when there is very limited salmon available to consume (off season).

For that, the minimum concentration of resource for both the consumers need to be compared at steady state.

Competition model: transient and steady state

Competition: Brown Bears vs. Bald Eagles



R^* → Minimum number of resource required to sustain a consumer population, that is the consumer population growth rate is zero (at equilibrium and does not change, especially negatively)

Minimum resource concentrations

R^* for Brown Bears:

$$R^*_{bears} = \frac{1}{\text{attack rate 1}} \times \frac{C_{max1} \times \text{death rate 1}}{C_{max1} \times E1 - \text{death rate 1}} \approx 15 \text{ resource units}$$

R^* for Bald Eagles:

$$R^*_{eagles} = \frac{1}{\text{attack rate 2}} \times \frac{C_{max2} \times \text{death rate 2}}{C_{max2} \times E2 - \text{death rate 2}} \approx 21 \text{ resource units}$$

With a lead on the plot for type II functional responses and also a lower R^* value, brown bears seem to actually prosper the transient as well as steady state dynamics in this competition.

Competition model: foraging efficiency as trait for trade-off



Rate of change of resource: Salmon

$$\frac{dR}{dt} = [r_{in} \times (K - R)] - [C_{max1} \times \frac{\text{attack rate } 1 \times R}{C_{max1} + (\text{attack rate } 1 \times R)} \times C1] - [C_{max2} \times \frac{\text{attack rate } 2 \times R}{C_{max2} + (\text{attack rate } 2 \times R)} \times C2]$$

$$\Rightarrow \frac{dR}{dt} = [\frac{1}{400} \times (20000 - 10000)] - [10 \times \frac{0.013 \times 10^4}{10 + (0.013 \times 10^4)} \times 30] - [3 \times \frac{0.0067 \times 10^4}{3 + (0.0067 \times 10^4)} \times 30]$$

$$\Rightarrow \frac{dR}{dt} = - 339.7 \text{ salmon per day}$$

A decrease of 3.397% per day in the resource



Rate of change of consumer 1: Brown Bears

$$\frac{dC1}{dt} = \alpha \times [E1 \times C_{max1} \times \frac{\text{attack rate } 1 \times R}{C_{max1} + (\text{attack rate } 1 \times R)} - \text{death rate } 1] \times C1$$

$$\Rightarrow \frac{dC1}{dt} = 0.5 \times [0.00068 \times 10 \times \frac{0.013 \times 10^4}{10 + (0.013 \times 10^4)} - 0.000137] \times 30 = 0.092 \text{ fraction of bears per day}$$

An increase of approx. 0.31% per day



Rate of change of consumer 2: Bald Eagles

$$\frac{dC2}{dt} = \beta \times [E2 \times C_{max2} \times \frac{\text{attack rate } 2 \times R}{C_{max2} + (\text{attack rate } 2 \times R)} - \text{death rate } 2] \times C2$$

$$\Rightarrow \frac{dC2}{dt} = 0.8 \times [0.00137 \times 3 \times \frac{0.067 \times 10^4}{3 + (0.067 \times 10^4)} - 0.0001826] \times 30 = 0.090 \text{ eagle per day}$$

An increase of 0.30% per day

Foraging efficiency is the ratio of energy gained from resource consumption to the energy expended in obtaining that resource. Brown bears, with a higher maximum consumption rate (Cmax) than bald eagles, face a trade-off in foraging efficiency, affecting factors like death rate and reproductive efficiencies.

For Brown Bears (alpha = 0.5):

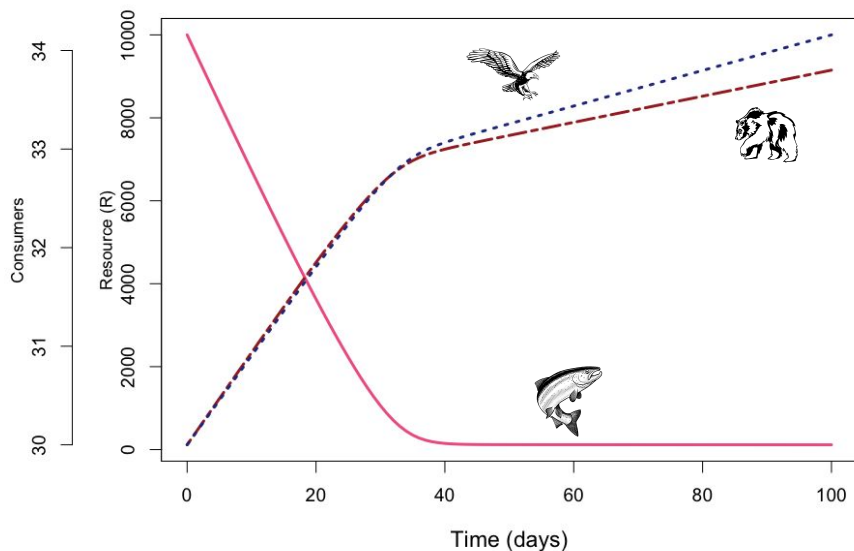
- Competition for prime catching spots among bears
- Need to maintain a strong presence at salmon-rich sites
- Exhaustion due to foraging in fast-running water currents

For Bald Eagles (beta = 0.8):

- Good at scavenging carrion
- Ability to make precise dives to catch salmon without much competition
- Diverse diet compared to brown bears

Competition model: foraging efficiency as trade-off trait

Competition: Brown Bears vs. Bald Eagles with foraging efficiencies



Legend

- Salmon (Resource)
- - - Brown Bears (Consumer 1)
- ... Eagles (Consumer 2)

Minimum resource concentrations with trade-off

R* for Brown Bears:

$$R^*_{bears} = \frac{1}{\alpha \times \text{attack rate } 1} \times \frac{C_{max1} \times \text{death rate } 1}{C_{max1} \times E1 - \text{death rate } 1} \approx 30.61 \text{ resource units}$$

R* for Bald Eagles:

$$R^*_{eagles} = \frac{1}{\beta \times \text{attack rate } 2} \times \frac{C_{max2} \times \text{death rate } 2}{C_{max2} \times E2 - \text{death rate } 2} \approx 26.16 \text{ resource units}$$

When foraging efficiencies are included, Bald Eagles seem to be relatively doing better than Brown Bears during the transient and steady states.

Inspiration: The Salmon Forest documentary <https://www.youtube.com/watch?v=rm25cRi8TL8&t=1178s>

Mathematical Biology

Weekly Exercise 4

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```
setwd("/Users/swati/Desktop/Mathematical Biology/")
library(deSolve)

# Organisms portfolio
# Resource: Salmon
# Consumer 1: Brown Bears
# Consumer 2: Bald Eagles

# All values used for calculations are arbitrary

# Defining the function for the competition model
comp_model <- function(time, state, params) {
  with(as.list(c(state, params)), {
    dC1 <- ((E1 * Cmax1 * (b1 * R / ((b1 * R) + Cmax1))) - death_rate_1) * C1
    dC2 <- ((E2 * Cmax2 * (b2 * R / ((b2 * R) + Cmax2))) - death_rate_2) * C2
    dR <- (r_in * (K - R)) - (Cmax1 * (b1 * R / ((b1 * R) + Cmax1)) * C1) - (Cmax2 * (b2 * R / ((b2 * R) + Cmax2)) * C2)
    return(list(c(dR, dC1, dC2)))
  })
}

# Amount of resource available

## estimate of total spawning salmon per season
## (different salmon species have different spawning seasons in a year)
R <- 10000

# average number of salmon swimming upstream per day to go to spawning grounds
input <- 300

# average rate of resource input into the stream per day of the season
r_in <- 1/300

# Maximum number of live salmon individuals that can be accommodated by the stream
K <- 20000

# Initial number of consumers living around the stream
C1 <- 30 # bears
C2 <- 30 # eagles

# Maximum consumption possible for each species
```



```

Cmax1 <- 10 # salmons per day for one bear
Cmax2 <- 3 # salmons per day for one eagle

# Number of births per year that leads to surviving consumer offsprings

## Birth rate per day if 2 bear cubs per year survive to adulthood (1 litter = 1 to 3 cubs)
birth_rate_1 <- (2/2)/365

## Birth rate per day if 2 eagle babies per year survive to adulthood (1 clutch = 1 to 3 eggs)
birth_rate_2 <- (2/2)/365

# Consumption required for each consumer per day as an essential resource during the season
consumption_1 <- 4 # if one bear needs to eat 4 salmon per day
consumption_2 <- 2 # if one eagle needs to eat one salmon per day

# Reproductive efficiency per day for each consumer species per unit of resource consumed
E1 <- birth_rate_1/consumption_1
E2 <- birth_rate_2/consumption_2

# # Attack rates per day
b1 <- consumption_1/input
b2 <- consumption_2/input

# Death rate of consumers per day
death_rate_1 <- 1/(20*365) # 1 bear dies in every 20-25 years
death_rate_2 <- 1/(15*365) # 1 eagle dies in every 15-25 years

# Steady-state dynamics for competition model
# Minimum resource concentration R* for brown bears
Rstar_C1 <- (1/b1)*((Cmax1*death_rate_1)/(Cmax1*E1-death_rate_1))
cat("Minimum required salmon concentration for Brown Bears =>", Rstar_C1)

## Minimum required salmon concentration for Brown Bears => 15.30612

# Minimum resource concentration R* for bald eagles
Rstar_C2 <- (1/b2)*((Cmax2*death_rate_2)/(Cmax2*E2-death_rate_2))
cat("\nMinimum required salmon concentration for Bald Eagles =>", Rstar_C2)

##
## Minimum required salmon concentration for Bald Eagles => 20.93023

# Set initial conditions, parameters and times
initial_state <- c(R = R, C1 = C1, C2 = C2) # Initial populations
parameters <- c(E1 = E1, E2 = E2, Cmax1 = Cmax1, Cmax2 = Cmax2,
                b1 = b1, b2 = b2, death_rate_1 = death_rate_1,
                death_rate_2 = death_rate_2,
                r_in = r_in, K = K)

times <- seq(0, 100, by=1)

```



```
# Applying the model
comp_sim <- ode(y = initial_state, times = times, func=comp_model, parms=parameters)
colnames(comp_sim) <- c("Time", "Resource", "Brown Bears", "Bald Eagles")
head(comp_sim)
```

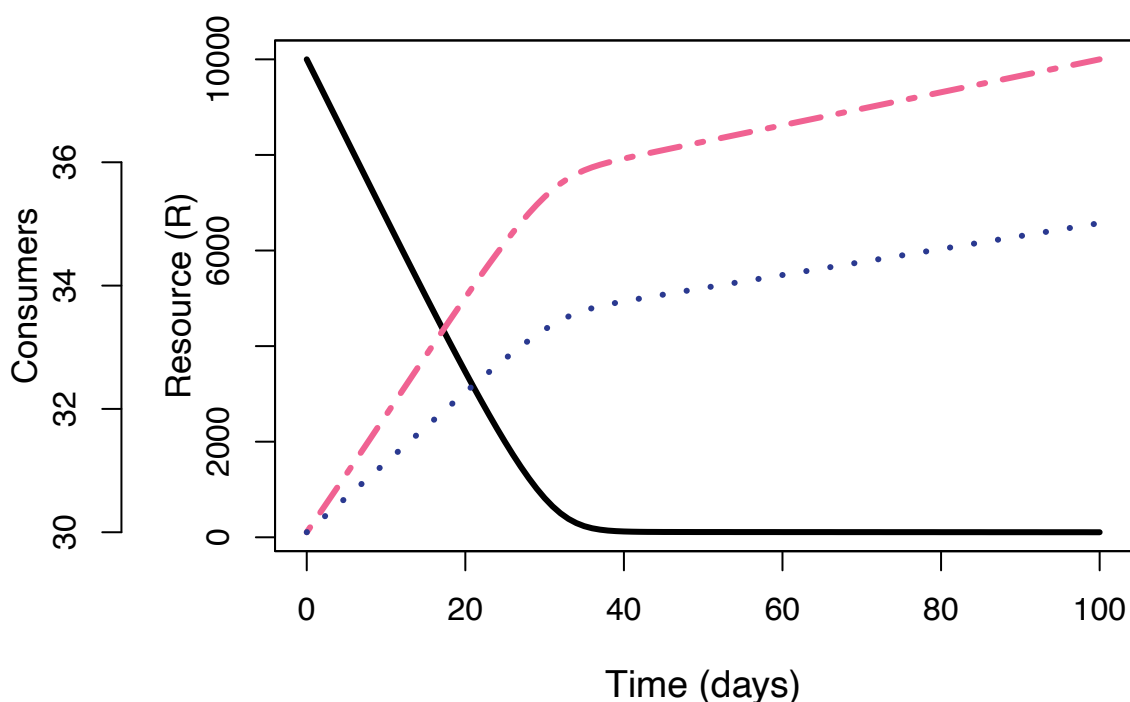
```
##      Time  Resource Brown Bears Bald Eagles
## [1,]    0 10000.000    30.00000    30.00000
## [2,]    1  9668.058    30.18739    30.11262
## [3,]    2  9335.976    30.37547    30.22549
## [4,]    3  9003.833    30.56421    30.33858
## [5,]    4  8671.669    30.75358    30.45189
## [6,]    5  8339.572    30.94352    30.56539
```

```
# Increasing the font size for axes annotations
# par(cex=1.2)
```

```
# Legend
Legend = c("Salmon (Resource)", "Brown Bears (Consumer 1)", "Eagles (Consumer 2)")
```

```
# Plotting the results
matplot.0D(comp_sim, which = list(c(1), c(2,3)),
            lty = c(1,6,3), col=c("black", "#f06292", "#2a3990"),
            lwd=c(3),
            xlab="Time (days)",
            ylab = c("Resource (R)", "Consumers"),
            main="Competition: Brown Bears vs. Bald Eagles",
            cex.lab=1.2,
            legend="none")
```

Competition: Brown Bears vs. Bald Eagles



```
# legend("topleft", Legend, lty = c(1,6,3), col=c("black", "#f06292", "#2a3990"),
#       lwd=c(3), title= "Legend")

# Incorporating foraging efficiency based on hunting and scavenging by consumers
# as single trait as trade-off between parameters.

## Foraging efficiency can be defined as the ratio of energy gained to
## energy expended to acquire food

# Foraging efficiency of brown bears
# Low due to competition from other bears
# and due to exhaustion caused by fighting for prime catching spots
alpha <- 0.5

# Foraging efficiency of bald eagles
# Higher due to less energy expended in hunting
# as scavenging of carrion works well for eagles during peak spawning season
beta <- 0.8

# Re-defining the function for the competition model
# with foraging efficiency as the single trait for trade-off
comp_model_2 <- function(time, state, params) {
  with(as.list(c(state, params)), {
    dC1 = alpha * ((E1 * Cmax1 * (b1 * R / ((b1 * R) + Cmax1))) - death_rate_1) * C1
    dC2 = beta * ((E2 * Cmax2 * (b2 * R / ((b2 * R) + Cmax2))) - death_rate_2) * C2
```

```

    dR <- (r_in * (K - R)) - (Cmax1 * (b1 * R / ((b1 * R) + Cmax1)) * C1) - (Cmax2 * (b2 * R / ((b2 * R) + Cmax2)) * C2)
    return(list(c(dR, dC1, dC2)))
  })
}

```

```

# Setting updated parameters

```

```

parameters2 <- c(E1 = E1, E2 = E2, Cmax1 = Cmax1, Cmax2 = Cmax2,
  b1 = b1, b2 = b2, death_rate_1 = death_rate_1,
  death_rate_2 = death_rate_2,
  r_in = r_in, K = K, alpha=alpha, beta=beta)

```

```

# Applying the extended model with foraging efficiencies

```

```

comp_sim_2 <- ode(y = initial_state, times = times, func=comp_model_2, parms=parameters2)

```

```

# Updating column names of model results

```

```

colnames(comp_sim_2) <- c("Time", "Resource", "Brown Bears", "Bald Eagles")
head(comp_sim_2)

```

```

##      Time Resource Brown Bears Bald Eagles
## [1,]    0 10000.000    30.00000    30.00000
## [2,]    1  9668.525    30.09355    30.09006
## [3,]    2  9337.839    30.18715    30.18026
## [4,]    3  9008.021    30.28079    30.27056
## [5,]    4  8679.100    30.37446    30.36097
## [6,]    5  8351.160    30.46812    30.45148

```

```

# Steady-state dynamics for competition model with foraging efficiency included

```

```

# Calculating R star for both consumers

```

```

# R* for brown bears

```

```

Rstar_C1 <- (1 / (alpha * b1)) * ((Cmax1 * death_rate_1) / (Cmax1 * E1 - death_rate_1))
Rstar_C1

```

```

## [1] 30.61224

```

```

# R* for bald eagles

```

```

Rstar_C2 <- (1 / (beta * b2)) * ((Cmax2 * death_rate_2) / (Cmax2 * E2 - death_rate_2))
Rstar_C2

```

```

## [1] 26.16279

```

```

# Increasing the font size for axes annotations

```

```

# par(cex=1.2)

```

```

# Plotting the results

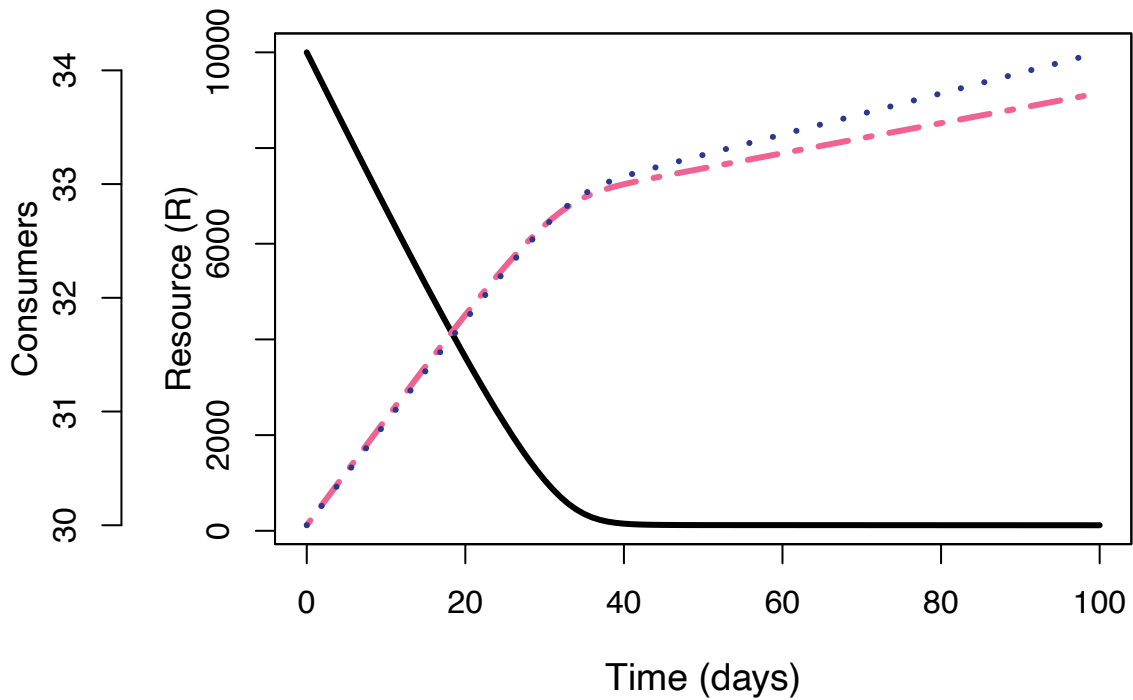
```

```

matplot.OD(comp_sim_2, which = list(c(1), c(2,3)),
  lty = c(1,6,3), col=c("black", "#f06292", "#2a3990"),
  lwd=c(3),
  xlab="Time (days)",
  ylab = c("Resource (R)", "Consumers"),
  main="Competition: Brown Bears vs. Bald Eagles with foraging efficiencies",
  cex.lab=1.2,
  legend="none")

```

Competition: Brown Bears vs. Bald Eagles with foraging efficie



```
# Printing results
if (Rstar_C1 < Rstar_C2) {
  cat("With foraging efficiency considered, Brown Bears prosper at lower salmon concentration of", Rstar_C1)
} else if (Rstar_C1 > Rstar_C2) {
  cat("With foraging efficiency considered, Bald Eagles prosper at lower salmon concentration of", Rstar_C2)
} else {
  cat("With foraging efficiency considered, Brown Bears and Bald Eagles have the same R* values and may coexist")
}
```

```
## With foraging efficiency considered, Bald Eagles prosper at lower salmon concentration of 26.16279
```