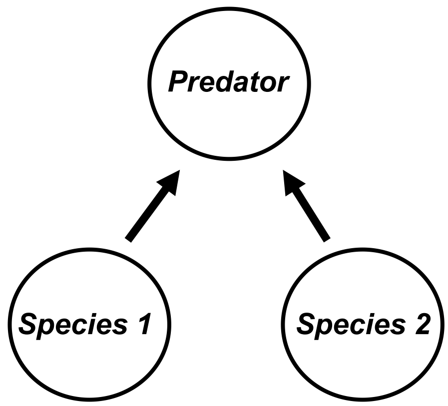
Introduction to Theoretical Ecology Assignment 9

Apparent Competition and P* Rule

In addition to exploitative competition, species can also compete indirectly via a common predator, known as “apparent competition”:



In this assignment, we are going to build a model of such interactions among two focal prey species (N_1 and N_2) and a predator (P) and simulate their population dynamics.

1. Assume that N_1 and N_2 grow exponentially with intrinsic growth rates r_1 and r_2 and are consumed by predator in a linear fashion at the rates a_1 and a_2. The conversion efficiencies for the two prey items to predator are e_1 and e_2, and the mortality rate of predator is m. Write out your model and simulate the system. Try out different combinations of parameter values and discuss if the two focal prey species can coexist. (Hint: There is a P* rule, just like the R* rule for exploitative competition.) (5 pts)

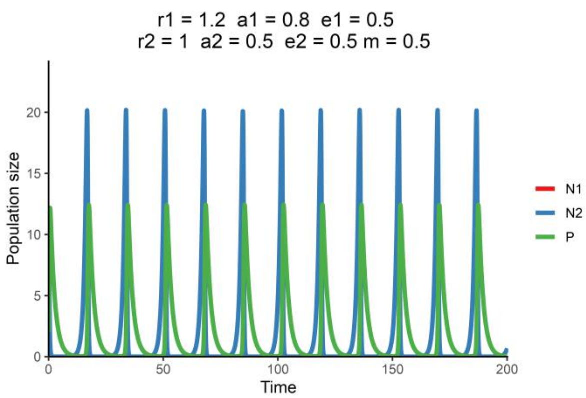
Solution

$$\frac{dN_1}{dt} = r_1N_1 - a_1N_1P$$

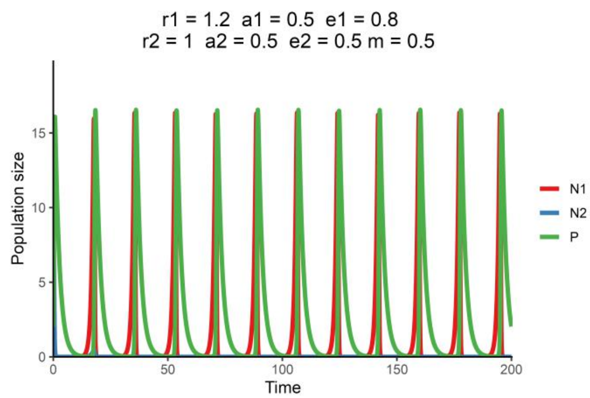
$$\frac{dN_2}{dt} = r_2N_2 - a_2N_2P$$

$$\frac{dP}{dt} = e_1a_1N_1P + e_2a_2N_2P - mP$$

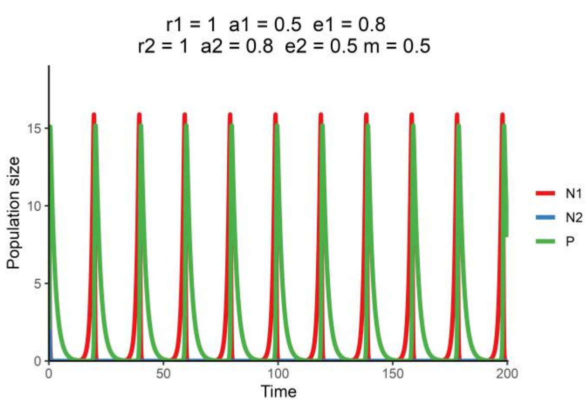
$r_1 > r_2$ and $a_1 > a_2$



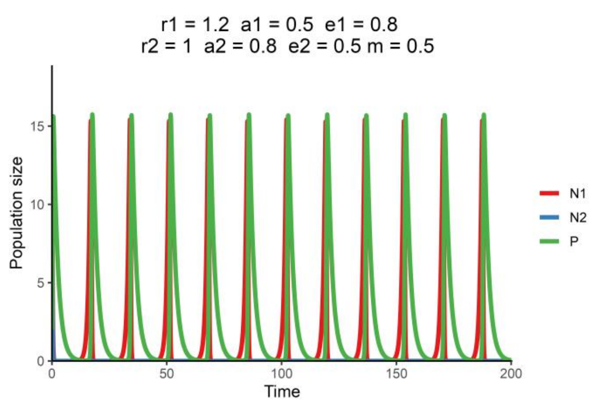
$r_1 > r_2$ and $e_1 > e_2$



$a_1 < a_2$ and $e_1 > e_2$



$r_1 > r_2$, $a_1 < a_2$, and $e_1 > e_2$



In this system, the two prey species cannot coexist. One species will be driven to extinction, and the original model would then reduce to the Lotka-Volterra predator-prey model where predator and the remaining prey exhibit neutral population cycles.

Paralleling the R* rule of exploitative competition for prey coexistence, there is also a P* rule for apparent competition: the dominant prey species under apparent competition would be the one with a high *r/a*, as it can both withstand and support higher predator numbers. To put it another way, when predator increases from rare, the species with a lower *r/a* will exhibit zero net growth first and the other with a higher *r/a* will survive.

R code

```
library(tidyverse)
library(deSolve)

Apparent_exp_func <- function(r1 = 1.2, a1 = 0.5, e1 = 0.5,
                              r2 = 1, a2 = 0.5, e2 = 0.5,
                              m = 0.5){
  Apparent_exp_model <- function(times, state, parms) {
    with(as.list(c(state, parms)), {
      dN1_dt = r1*N1 - a1*N1*P
      dN2_dt = r2*N2 - a2*N2*P
      dP_dt = e1*a1*N1*P + e2*a2*N2*P - m*P
      return(list(c(dN1_dt, dN2_dt, dP_dt)))
    })
  }

  times <- seq(0, 200, by = 0.1)
  state <- c(N1 = 10, N2 = 10, P = 2)
  parms <- c(r1 = r1, a1 = a1, e1 = e1,
             r2 = r2, a2 = a2, e2 = e2,
             m = m)

  pop_size <- ode(func = Apparent_exp_model, times = times, y = state,
parms = parms)
```

```
  pop_size %>%
    as.data.frame() %>%
    pivot_longer(cols = -time, names_to = "species", values_to = "N")
%>%
    ggplot(aes(x = time, y = N, color = species)) +
    geom_line(size = 1.5) +
    theme_classic(base_size = 12) +
    labs(x = "Time", y = "Population size") +
    scale_x_continuous(limits = c(0, 200.5), expand = c(0, 0)) +
    scale_y_continuous(limits = c(0, max(pop_size[, -1])*1.2), expand
= c(0, 0)) +
    scale_color_brewer(name = NULL, palette = "Set1") +
    labs(title = paste("r1 =", r1, " a1 =", a1, " e1 =", e1, "\n",
                       " r2 =", r2, " a2 =", a2, " e2 =", e2,
                       "m =", m)) +
    theme(plot.title = element_text(hjust = 0.5))

}

Apparent_exp_func(r1 = 1.2, a1 = 0.5, e1 = 0.8,
                  r2 = 1, a2 = 0.5, e2 = 0.5,
                  m = 0.5)
Apparent_exp_func(r1 = 1.2, a1 = 0.5, e1 = 0.8,
                  r2 = 1, a2 = 0.5, e2 = 0.5,
                  m = 0.5)
Apparent_exp_func(r1 = 1, a1 = 0.5, e1 = 0.8,
                  r2 = 1, a2 = 0.8, e2 = 0.5,
                  m = 0.5)
Apparent_exp_func(r1 = 1.2, a1 = 0.5, e1 = 0.8,
                  r2 = 1, a2 = 0.8, e2 = 0.5,
                  m = 0.5)
```

2. Now consider N_1 and N_2 grow logistically with carrying capacities K_1 and K_2. Again, write out your model, simulate the system, and discuss if the two prey species can coexist. What is the difference between this and the previous model? Can you explain why? (5 pts)

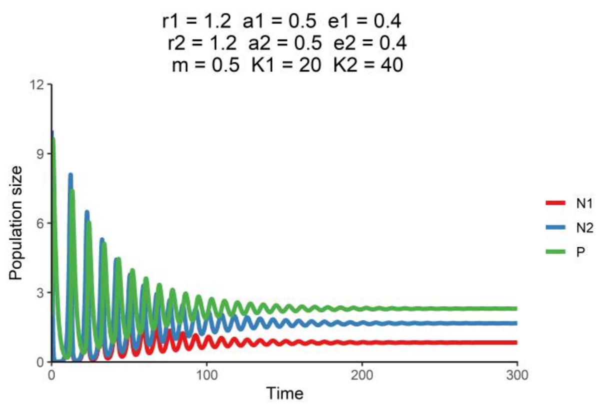
Solution

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1}{K_1}) - a_1 N_1 P$$

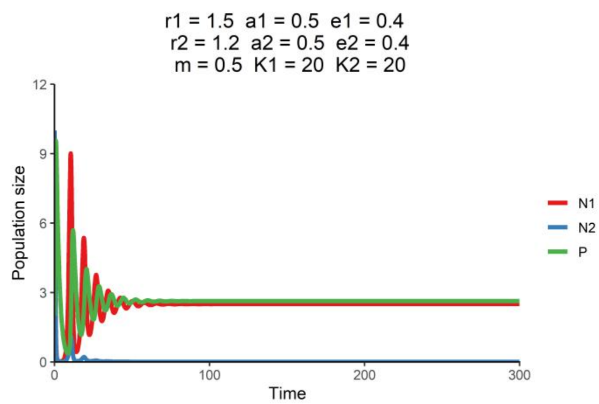
$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2}) - a_2 N_2 P$$

$$\frac{dP}{dt} = e_1 a_1 N_1 P + e_2 a_2 N_2 P - mP$$

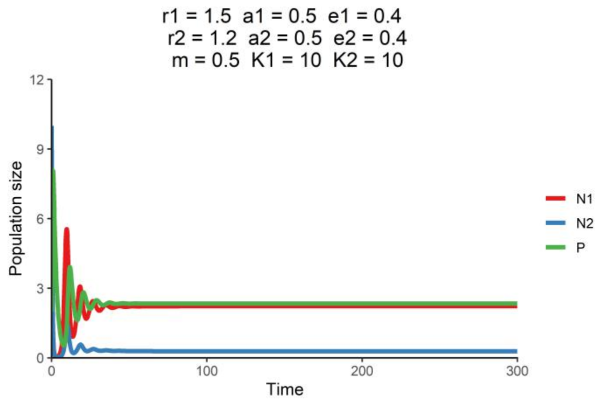
$K_2 > K_1$



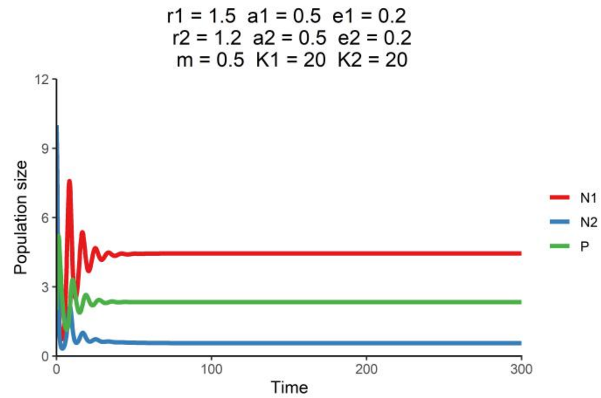
$r_1/a_1 > r_2/a_2$



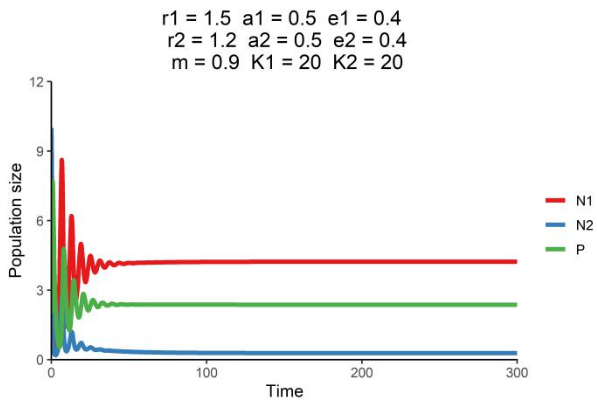
$r_1/a_1 > r_2/a_2$ with lower K_1 and K_2



$r_1/a_1 > r_2/a_2$ with lower e_1 and e_2



$r_1/a_1 > r_2/a_2$ with higher m



When the two prey species exhibit logistic growth, they are able to coexist under certain parameter settings. In particular, lower carrying capacity K, higher predator mortality m, and lower conversion efficiency e could facilitate coexistence of the two species that may otherwise undergo competitive exclusion. This suggests that self-regulation of prey populations (logistic growth rather than exponential growth) is critical for species coexistence, and stronger prey self-regulation (i.e., lower K; greater intraspecific effect) as well as reduced predator growth (lower e and higher m) would help stabilize the system.

R code

```
library(tidyverse)
library(deSolve)

Apparent_logistic_func <- function(r1 = 1.2, a1 = 0.5, e1 = 0.5,
                                   r2 = 1, a2 = 0.5, e2 = 0.5,
                                   m = 0.5, K1 = 50, K2 = 50){
  Apparent_logistic_model <- function(times, state, parms) {
    with(as.list(c(state, parms)), {
      dN1_dt = r1*N1*(1-N1/K1) - a1*N1*P
      dN2_dt = r2*N2*(1-N2/K2) - a2*N2*P
      dP_dt = e1*a1*N1*P + e2*a2*N2*P - m*P
      return(list(c(dN1_dt, dN2_dt, dP_dt)))
    })
  }

  times <- seq(0, 300, by = 0.1)
  state <- c(N1 = 10, N2 = 10, P = 2)
  parms <- c(r1 = r1, a1 = a1, e1 = e1,
             r2 = r2, a2 = a2, e2 = e2,
             m = m, K1 = K1, K2 = K2)

  pop_size <- ode(func = Apparent_logistic_model, times = times, y =
state, parms = parms)

  pop_size %>%
    as.data.frame() %>%
    pivot_longer(cols = -time, names_to = "species", values_to = "N")
%>%
    ggplot(aes(x = time, y = N, color = species)) +
    geom_line(size = 1.5) +
    theme_classic(base_size = 12) +
    labs(x = "Time", y = "Population size") +
    scale_x_continuous(limits = c(0, 300.5), expand = c(0, 0)) +
    scale_y_continuous(limits = c(0, max(pop_size[, -1])*1.2), expand
= c(0, 0)) +
    scale_color_brewer(name = NULL, palette = "Set1") +
    labs(title = paste("r1 =", r1, " a1 =", a1, " e1 =", e1, "\n",
                       " r2 =", r2, " a2 =", a2, " e2 =", e2, "\n",
                       "m =", m, " K1 =", K1, " K2 =", K2)) +
    theme(plot.title = element_text(hjust = 0.5))

}
```

```
Apparent_logistic_func(r1 = 1.2, a1 = 0.5, e1 = 0.4,
                       r2 = 1.2, a2 = 0.5, e2 = 0.4,
                       m = 0.5, K1 = 20, K2 = 40)
Apparent_logistic_func(r1 = 1.5, a1 = 0.5, e1 = 0.4,
                       r2 = 1.2, a2 = 0.5, e2 = 0.4,
                       m = 0.5, K1 = 20, K2 = 20)
Apparent_logistic_func(r1 = 1.5, a1 = 0.5, e1 = 0.4,
                       r2 = 1.2, a2 = 0.5, e2 = 0.4,
                       m = 0.9, K1 = 20, K2 = 20)
Apparent_logistic_func(r1 = 1.5, a1 = 0.5, e1 = 0.2,
                       r2 = 1.2, a2 = 0.5, e2 = 0.2,
                       m = 0.5, K1 = 20, K2 = 20)
Apparent_logistic_func(r1 = 1.5, a1 = 0.5, e1 = 0.4,
                       r2 = 1.2, a2 = 0.5, e2 = 0.4,
                       m = 0.5, K1 = 10, K2 = 10)
```